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FACTORS CAUSING DECLINE IN SOCKEYE SALMON OF KARLUK RIVER, ALASKA

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ABSTRACT

Cyclic fluctuations in the sockeye salmon runs of Karluk River (Alaska) coincide with those of adjacent streams, indicating that these fluctuations have a common cause. After removal from the records of the broods the variation in the returns caused by various climatic and biological factors, it is clear that the sockeye salmon have a dome-shaped reproduction curve. The general decline in abundance can be ascribed to a lower survival rate from spawner to returning adults in recent years. There is evidence that this lowered survival rate results partially from seasonal distribution of escapement and partially from heightened mortality of the young during fresh-water residence. Smolt populations in a 15-year period, ranging in numbers from 4,700,000 to 13,200,000, show a linear relation with total weight of the whole smolt biomass indicating that within this range competition for food between young of the same brood in the lake is of no importance. At least a portion of the general decline is tentatively ascribed to heightened predation in recent years since destruction of the former cyclic character of the runs has lessened natural control of predators through a reduced amplitude of the oscillations in number of spawners.

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FACTORS CAUSING DECLINE IN SOCKEYE SALMON OF KARLUK RIVER, ALASKA

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Karluk River with its connecting lakes is the gest of several highly productive sockeye-mon (*Oncorhynchus nerka*) streams in the north-st and southwest portions of Kodiak Island . 1). Because this important fishery has con-ued to decline over many years, it has been the ject of much study by the Fish and Wildlife vice and its predecessors.

pose of the Study

The sockeye salmon run of Karluk River was cted for this detailed study for three reasons: this valuable run has continued to decline pite efforts to maintain it by providing an equate number of spawners, (2) at no other ality do we possess such a long series of ob-vations on the numbers of fish in the run, mbers of spawners, ages of seaward migrants l returning adults, concomitant data of the ery, and the limnology of the nursery lake, and because of the great variation in both fresh ter and ocean residence of the Karluk River keye salmon the study promised to yield in-mation of great value in deducing principles general applicability to management of salmon ources.

Although several types of data are available, se are insufficient in some respects to fully wer some of the pertinent questions. Never-less, in this analysis we have sought to postu-reasonable hypotheses to explain the ob-ved facts. This has been done in order to rd a basis for action in accordance with the wledge now available. There are several nts requiring additional research, the results which may modify some of the explanations en herein. Meanwhile the conclusions and otheses advanced furnish a basis both for the nning and execution of further research and immediate action toward arresting and per-s reversing the long downward trend of an portant salmon resource.

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History of the Karluk Investigations

The scientific investigations were not placed on a continuous and systematic basis until 1921. However, such was the importance of the Karluk fisheries that studies were commenced as early as the summer of 1889, when the United States Fish Commission sent Dr. Tarleton H. Bean to Alaska. He spent from August 2 to September 27 at Karluk, and August 17 to 21 at Karluk Lake. In this first published report (Bean 1891) on the Karluk salmon runs he describes the spawning in various streams and includes a reconnaissance survey of Karluk Lake and a portion of Karluk River. He took samples of young fish to determine the hatching dates, sampled the other fishes, and made a series of temperature observations.

Early data on Karluk may be placed in two categories, (1) the description of the fishing and records of the catches and (2) information on the spawning in Karluk Lake, its tributaries, and Karluk River by the few persons who undertook the arduous hike over muskeg and up the shallow winding river to the lake. After the 1889 reconnaissance survey of Tarleton Bean 14 years elapsed before the lake was again visited in 1903 by Cloudsley Rutter. Although he spent some time at the lake, the description given from his notes by Chamberlain (1907) is very brief. Notes on short visits to the lake by Ward T. Bower in 1911, Edward M. Ball in 1917, and by Henry O'Malley and Charles H. Gilbert in 1919 are given by Gilbert and Rich (1927). The first rather complete survey of the spawning grounds was made by O'Malley and Gilbert in 1921. Thereafter (with the exception of 1923 and 1925) the lake has been visited each year.

In 1926 Willis H. Rich with a small field party made an accurate survey of the lake, including soundings, and commenced the collection of limnological data published in 1932 (Juday, Rich, Kemmerer, and Mann) for the 1926–30 period.

FIGURE 1.—Map of Karluk Lake and vicinity.

The early statistics of Karluk and notes on the fishery were collected by A. B. Alexander, fishery expert on the Fish Commission steamer *Albatross* in 1898 and 1899 (Moser 1899, 1902). The statistics of the fishery up to 1927 are given in Rich and Ball (1931).

In 1921 a weir for counting adult salmon on their upstream migration was placed in the river at the head of the lagoon and maintained the until 1941. From 1942 to 1944 it was install about 20 miles up the river near the head of Lars Bay. Since 1945 it has been operated at a si about 300 yards below the outlet of Karluk Lak The principal reasons for finally locating the we at the lake outlet instead of farther down the riv were the difficulty in maintaining it when hi

er brought down excessive quantities of aquat-weeds, and (in the even-numbered years) the gging of the weir by the carcasses of thousands pink salmon (*Oncorhynchus gorbuscha*) that wn chiefly in the river below the lake.

eral life history of Karluk sockeye

The general life history of the Karluk River keye salmon has been well established by Gil-t and Rich (1927) and Barnaby (1944) from ensive data collected continuously since 1921. e chief features are portrayed in figure 2. In r 0 the parents (of several age groups) ascend river, spawn in the streams tributary to Karluk ke and in the lake itself, and die. The spawn-may commence late in June and continue until in the fall. The great majority of the fish in early run spawn in the tributary streams, large small; a few spawn on gravelly beaches in the e itself. Those ascending the Karluk after the of July spawn both on the lake beaches and the stream gravels, but the larger tributaries preferred. It is estimated (Nelson and Ed-ndson, 1955) that about 75 percent of all the wners use the streams, the remaining 25 per-t the lake beaches. In some years, a few usand late-arriving sockeye spawn in the main rluk River below the outlet of the lake.

The eggs hatch during late winter or early ing, but the fry remain buried in the gravel il they have absorbed the yolk sac. During following spring and summer, after absorbing yolk, the fry struggle up out of the gravel; se in the tributary streams descend into the e. We are not certain what happens to the from nests in the main river below the lake. The races of sockeye spawning below Chilko Lake in the Fraser River system for instance, habitually spawn below a lake, and the young must swim upstream into the lake. At Karluk, although the spawning below the lake has not been generally regarded as a regular occurrence, large numbers may spawn here in some years. (See appendix L.)

Although some of the young probably drift down the river to produce the few sea-type fish found in the returns, Philip Nelson writes that he has witnessed this group of young working upstream through the weir pickets. The observations of Johnson (1956) on the upstream movements of sockeye fry hatched below Babine Lake are strong confirmation of this habit.

The majority of the fry (fig. 2) reach the lake and live a pelagic existence for a varying length of time. Most of them leave the lake in the late spring and early summer (late May through July) of their third or fourth year of life. Extensive marking experiments have shown that the survival during their sojourn at sea, which may vary from less than 1 to 4 years, approaches 20 percent. Survival is higher for the older and slightly larger 4-year smolts than for the 3-year smolts.

The adults from the spawning of one year will return to the river from 3 to 8 years later after spending 0 to 4 summers in the lake and less than 1 to 4 summers at sea. The majority normally return as mature adults in their fifth year.

The runs at Karluk occur over an usually long period of time. The first sockeye may start running in mid-May and the last of the run may be entering the river in October.

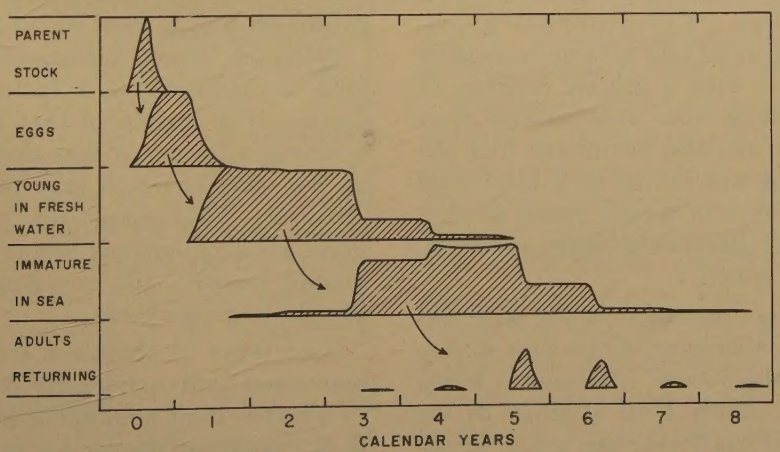

FIGURE 2.—Time diagram of life history stages.

Scope of the report

Because of the large amount of data available, and the necessity of showing how it was treated to prepare it for analysis, the bulk of the detailed data have been placed in the appendix to this report so as not to interfere unduly with the presentation of the analyses.

The first step was to define the field by determining what catches of sockeye salmon could be logically attributed to the Karluk population. Following this it was necessary to determine whether the short-term fluctuations in the Karluk runs occurred only in that stream or simultaneously in adjacent areas.

After it was established that the sockeye runs in Karluk and the neighboring streams exhibit concomitant fluctuations in abundance, analyses were made to determine the effect on freshwater survival of various climatic factors; and to remove these effects from the data to discover the true character of the sockeye reproduction curve. In addition to the variations in reproductive success induced by climatic fluctuation, the removal of the climatic effects from the data made it possible to observe another effect, viz., a significant difference in survival between broods spawned in even- and odd-numbered years, which has been attributed to the great disparity in abundance between the even- and odd-year pink salmon populations that apparently compete for spawning space with the sockeye.

Having also adjusted the data to discount the effects on sockeye survival of the 2-year cyclic variation in pink-salmon abundance, the adjusted data for survival according to number of spawners were now analyzed to determine the nature of the reproduction curve. The result was a constantly decreasing survival rate with an increasing number of spawners; with a greater number of spawners, the returning runs were smaller than the parent runs. It was also discovered that the decline in recent runs was caused by a lower rate of survival per spawner in recent years, so that the decline continued despite the large proportion of fish permitted to spawn.

Another phenomenon apparent in the data was the persistent cyclic character of the runs during the earlier years of the fishery. Because it was a 5-year cycle it has usually been ascribed to the normal dominance of the 5-year age group in the mature adults. However, analysis shows that because of the changes in survival rate with th number of spawners, coupled with the variation in age composition of the runs, this explanatio is untenable. The persistence of the cycle despite fluctuations in climatic and other factors indicated that it was density-dependent. Analysi shows a significant negative relation between th density of young in the lake (young in their thir and fourth years) and the survival of broods tha were in the lake as fry during the same yea Since the 3- and 4-year olds average 2½ year older than the fry the result is a negative 2½ yea correlation between runs, thus accounting for th positive 5-year cycle.

The reasons for the long-term decline in abun dance are discussed from the standpoint of physica and biological factors. The small extent of th spawning beds in relation to the lake area fo growth of the young is considered a factor in de termining the decreased survival per spawner a the number of spawners increases.

An analysis of the numbers and weights of th seaward-migrating smolts shows that the de creased survival cannot be ascribed directly t intraspecific competition for food. The fact tha the largest broods have the largest individua smolts indicates that the relative survival of eac year class may be at least partially dependent o the annual food density so that survival is highes when growth is fastest.

The individual size, number, and total biomas of the smolts are compared for Karluk and Cultu Lakes. It would appear that the much greate growth rate of Karluk smolts may be partiall caused by the fact that the high summer tempera tures restrict the Cultus Lake smolts to the hy polimnion during most of the growing season.

Although direct intraspecific competition fo food is dismissed as a factor in the long-ter decline, it is postulated that there is neverthele a strong influence of lake density of older youn on fry survival which may take the form of ca nibalism. This competition preserved the 5-yea cycle as the numerous young from the dominan broods lowered the survival from the small broods, and vice versa.

Two types of predators are discussed, densit dependent and nondensity-dependent, accordin to whether their abundance is or is not controlle to a significant degree by the abundance of th salmon. The nondensity-dependent type tend t

ke a fixed amount of salmon. This may have nded to accentuate the cyclic character of the ns during the early years since they reduced rvival from small runs, while for the very large ns a small reduction, especially of the spawning lults, would tend to increase total survival. or the small runs of recent years the nondensity-pendent predators would render it difficult to otain good survival until the number of spawners assed a threshold for which the amount taken by e predators would have little influence.

The density of the young coho salmon residing Cultus Lake in British Columbia has been own to be dependent on the density of young ckeye salmon. At Karluk the average number adult coho spawners entering the lake aver-ged 8,800 over a 9-year period indicating high otential predation by young cohoes.

Both the lake-residing arctic charr, *Salvelinus pinus* and the anadromous Dolly Varden charr, *alvelinus malma*, are abundant at Karluk. More an 80,000 of the latter have been trapped and estroyed at the weir during their annual down-ream migration in a single season.

If we postulate that these fish predators are ensity-dependent on young sockeye, it is ap-arent that the cyclic nature of the sockeye runs uring the earlier years could have effectively ntrolled their abundance. During the earlier eriod of 42 years (1887–1928) the amplitude of e oscillations between high and low numbers of ckeye spawners was more than twice as great in the following 25-year period (1929–53).

A fourth important factor influencing the sur-val rate per spawner is the effect on mortality the age at which the parr transform into smolts nd migrate seaward. Multiple regression analysis average smolt lengths, temperatures, numbers smolts migrating, and total biomass of the nolt migrations, shows that the threshold-size r the parr to transform into smolts is chiefly ependent on the number of fish in the total omass. Thus, the higher the lake density of oung, the younger (and smaller) are the migrat-g smolts. This implies a longer lake residence, nd therefore lower survival, of the young from naller broods.

In seeking for confirmation or denial of the regoing hypotheses a study was next made of rtain phases of the life history of the sockeye.

Analysis of seasonal occurrence of the runs over the 30 years from 1921–50 showed the sockeye entering the river from mid-May to mid-October. Three peaks of abundance occurred, the first and most evident peak is in mid-June, the second from late July to early August, and the third in early September.

The seasonal age composition of the runs was then studied. This showed that the seasonal occurrence of each age group is rather distinctive. The relative period during the season when each age group enters the river is governed by two factors: fresh-water age and ocean age. Except for the very few adults that entered the sea as fry, the age at the time of downstream migration has a negative effect on the season of return; the 2-year migrants return first, followed by the 3-, 4-, and lastly, the 5-year migrants.

The ocean age, however, has a contrary effect. The fish spending 4 seasons in the sea run first, followed by the 3-, 2-, 1-, and 0-ocean age groups.

Of the 18 commonly occurring combinations of fresh-water and ocean-age fish, only 8 groups are sufficiently numerous to contribute substantially to the run. These eight include all age groups in which the fish migrated seaward in their second to fourth year and spent 1 to 3 seasons in the ocean.

Analysis of the size of smolts leaving the lake shows that within any one season's migration the larger smolts of each age group migrate first. Marking experiments by Barnaby (1944) show that within each age group of smolts those leaving the lake earlier in the season tend to remain a shorter time at sea. The 4-year smolts also tend to stay at sea for a shorter period than the 3-year smolts. Thus it becomes apparent that the fastest-growing smolts are first to reach maturity.

The possibility of two or more distinct races of sockeye at Karluk is explored and rejected on present evidence, since it can be demonstrated that the peaks of seasonal occurrence in the run can be fully explained by the distinctive patterns of seasonal occurrence of fish belonging to the various age groups. Furthermore, it can be shown by correlation analysis that there is a significant relation in the abundance of fish of the same brood year maturing at different ages and running in different parts of the season in the same or the following calendar year.

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A study of the average age at maturity for the brood years of 1919–42 confirms the conclusion of Barnaby (1944) for a shorter period of time (1920–29) that the age at maturity has been increasing in recent years.

An explanation of this phenomenon of increasing age is found in the relation of brood size (mature adults) to age at maturity. The number of 5-year old fish is positively correlated with brood size ($r=0.78$, while the numbers of 6- and 7-year-old fish are negatively correlated ($r=-0.78$ and -0.60, respectively). Thus, this negative relation between average-age and brood-size is the result of the young of the smaller broods (accentuated in recent years by declining abundance) tending to remain an additional year in the lake.

Since man is the chief predator of the salmon run, an analysis was made to discover whether his manner of fishing could affect the survival rates per spawner. The chief portion of his catch has been consistently taken from the center portion of the run, leaving the very early and very late migrating fish almost untouched. No indication exists that this has had any effect on the seasonal occurrence of the runs, but it is postulated that this may have decreased the return per spawner, since the eggs and fry from very early or very late spawning were shown to be more likely to be affected by unfavorable climatic conditions.

The remainder of the report discusses in some detail the pros and cons of various hypotheses that have been advanced in the past to explain the dwindling runs, and advances hypotheses which appear to be supported by the data.

RELATION BETWEEN RUNS OF KARLUK AND OTHER LOCALITIES

Before proceeding with an analysis of the Karluk runs there are two questions which need to be answered. First, are the records of catches of Karluk River sockeye sufficiently accurate for our purpose? Second, if we are satisfied on the first point, do we find the fluctuations at Karluk to be unique, or is there a significant relation between fluctuations in abundance in Karluk and in adjacent streams that indicates a common cause of variation?

Catch allocations between Karluk and adjacent rivers

Accurate records of the catches of sockeye that are bound for the Karluk River are very important to any study of the causes for shifts in abundance of the runs. The catches of Karluk sockeye as given in the available records, apart from any minor discrepancies, are subject to two principal sources of possible error.

1. Inclusion in the early Karluk records of salmon taken in adjacent rivers. In this regard Rich and Ball (1931, p. 665) state,

> In 1896 * * * For the first time salmon were reported from Uganik, "Ayagulik" (probably intended for Ayakulik or Red River,) Kaguayak, and Little River, but the estimated catches at these places were excluded from the Karluk catch. It is believed, however, that in several years before and after 1896, Karluk catch statistics were slightly in error due to the inclusion of fish taken at other localities, but no attempt has been made to correct this except as indicated in the footnotes following table 14.

2. Possible errors in determining the destination of salmon caught in salt water at some distance from the rivers.

As to the first point, we have estimated the catches for Little River, Uganik River, and Red River prior to 1903, for the years in which they were included in the published totals for Karluk and have subtracted them. These estimated catches are likely minimal since they are based (table 3) on the best 5-year average catch, which of course, was made at a later period when these fisheries had been fully exploited for a number of years. The dates of 1888 for the commencement of fishing at Little River and Uganik River and of 1889 for the Red River are from the reports of Moser (1899, 1902). It will be noted as a result that the figures for Karluk production prior to 1903 are slightly less in some years than those given by earlier authors.

As to the second point Barnaby (1944) includes as Karluk sockeye all fish caught between Cape Karluk, about 3 miles west of the mouth of the Karluk River, and West Point, about 6 miles inside the western shore of Uganik Bay and about 75 miles northeasterly from the mouth of the Karluk River.

Catches could be allocated with confidence to particular rivers during the earlier years of the salmon fisheries when the catches were made chiefly with beach seines close to the mouths of the streams, or as at Karluk, in brackish lagoons at their mouths. After the advent of purse seines, gill nets, and traps the chances for taking salmon in one area bound for more than one stream were increased. In 1926 and 1927 traps were

aced near Broken Point just inside of Uganik ıy on the western shore and it was immediately spected that they were largely taking Karluk lmon. Accordingly, Rich and Morton (1929) gged and released 700 sockeye salmon at Broken int on August 19 and 20, 1927, to determine the stination of these fish (see table 1).

On the basis of this tagging experiment it was ncluded that all sockeye captured between Cape arluk on the west and West Point to the north- st should henceforth be considered as bound for e Karluk River and be included in the catch of at river. There could be several objections to is allocation on the basis of this lone experiment, nich can be summarized:

1. The experiment was performed so late in the ason as to yield no information on the earlier ns (76 percent of the Karluk run is normally er by the week ending August 23).

2. Because the Red River run was temporarily a very low ebb, the Red River fishery was closed fishing for several years, including 1927, so at no tags could be recovered there, and had e area been open, the number of tags recovered ring 1927 would have been less than in years normal-size runs.

3. Three tags were recovered at Alitak, beyond the Red River area, indicating that there might have been more bound for the Red River area.

4. Seven tags were recovered in Cook Inlet, Raspberry Strait, and Viekoda Bay, all east of the point of tagging, suggesting that some of the fish may have passed the mouth of the Karluk River traveling eastward.

5. Thirteen tags were taken in the southern arm of Uganik Bay from fish that were probably bound for Uganik River, a sockeye stream in the east arm of Uganik Bay. This run, like that of the Red River, was at a low ebb during the period embracing 1927. In the 23-year period from 1889 to 1911 the catch from Uganik Bay, which at that period was not taken by traps and presumably was made near the head of the bay, ranged from a low of 22,000 in 1897 to a high of 366,000 in 1896. The average catch was 123,000 sockeye with only 6 years falling below 100,000. By 1925, the last year before the traps were driven on the west shore near Broken Point, the catch was only 4,646. A weir was maintained in the Uganik River from 1928 to 1932, inclusive. During this 5-year period the average escapement up the river was only 24,609 sockeye salmon.

ABLE 1.—*Tagging experiments on sockeye salmon, 1922 to 1929, showing recoveries either on Kodiak-Afognak Islands, or from localities beyond* [1]

Locality of release	Date of release			Number released	Locality of recapture								Total recaptures	Percent moving to or beyond Kodiak Island
	Month	Day	Year		Cook Inlet	Afognak Island [2]	Uganik Bay	Uganik to Uyak Bay [3]	Uyak Bay	Karluk	Alitak	?		
ALASKA PENINSULA														
ga Island	June	30	1922	601	4								54	7.4
Do	do	2–5	1923	120									13	0
Do	do	7	1923	575		1							105	1.0
Do	do	23	1923	499									213	0
Do	do	26	1923	499									110	0
Do	do	27	1923	137	1								53	1.9
Do	do	27	1923	859	1					1			277	.7
Do	July	4	1923	110									43	0
Do	do	6	1923	633	1						1		172	1.2
cholaski Spit	do	11–17	1928	461	1		1	1					30	10.0
COOK INLET														
at Island	June	14	1929	127				3					29	10.3
Do	do	27	1929	45									10	0
Do	July	23	1929	18									7	0
ubble Point	June	26	1929	138		1		2					46	6.5
Do	July	18	1929	13									5	0
UGANIK BAY														
oken Point	August	19–20	1927	700	2	5	67	132	107		3	1	[4] 317	
TOTAL RECOVERIES														
aska Peninsula				4494	8	1	1	1		1	1		1070	1.2
ok Inlet				341		1		5					97	6.0

[1] Gilbert (1923), Gilbert and Rich (1925), Rich and Morton (1929), Seton Thompson (1930).
[2] Includes Afognak Island, Raspberry and Malina Straits, and Viekoda Bay.
[3] Includes Cape Ugat and Little River.
[4] 86 additional tags seen on salmon passing Karluk weir.

6. Tagging experiments in Cook Inlet and along the south side of the Alaska Peninsula (table 1) showed that 6 percent of the former and 1.2 percent of the latter moved to localities either on or beyond Kodiak-Afognak Islands.

7. It has been shown in several tagging experiments (Gilbert and Rich, 1925, and O'Malley and Rich, 1919) that the speed of migration increases considerably as the season advances. For this reason, the early-running fish spending a longer time en route are more subject to capture in areas far from their destination. Thus for the Fraser River runs (Rounsefell and Kelez, 1938) the traps took a larger share of the sockeye in years when the runs were early. When the runs were late the fish apparently hurried through the main channels, as only traps along the main route caught a fair share of the run. It is fair to assume that a larger share of the Karluk fish of the early run might be taken elsewhere, and it can only be conjectured as to whether the early arriving fish from other areas taken at Karluk are closely equal in numbers to the early Karluk fish taken elsewhere.

8. After stating that the Alitak fishery seems to be independent of other areas, Rich and Ball (1931) append a footnote saying,

> It has been noted in the past year or two, however, that many of the fish passing through the weirs in this district bear the marks of gillnets. Just where the Olga Bay fish pass through a gill-net fishery is not definitely known but it seems probable that it is along the northwest coast of Kodiak Island.

Despite all objections to the method used for allocating sockeye catches to the Karluk River there is considerable justification for the assumption that the resulting allocations were fairly accurate, at least for the 1904–25 period. The numbers of fish bound for mainland areas taken on Kodiak-Afognak Islands would seem from the tagging experiments to be fairly small. Since, on the other hand, a few of the island-bound salmon are probably taken on the mainland, the total error introduced by these catches must be relatively minor (table 2).

The only sizeable errors would have to come from misallocation of catches of sockeye made in the waters of the islands. Some idea of the relative importance of the sockeye streams can be gained from table 3 showing the areas of the lakes

TABLE 2.—*Catches of sockeye salmon at Karluk and nearby areas*

[In thousands]

Year	Karluk adjusted [1]	Area 5 Little River	Area 4 Uganik River	Area 9 Red River	Area 3 Kup-reanof Strait	Area 2 Rasp-berry Island and Malina Bay	Karluk total run
1882	59						
1883	189						
1884	282						
1885	469						
1886	646						99
1887	1,005						1,54
1888	2,631	*50	*100				4,04
1889	3,056	*106	220	*250			4,70
1890	2,580	*106	191	*463			3,96
1891	2,932	*106	131	*463			4,51
1892	2,140	*106	*143	*463		[3]	3,29
1893	2,198	*106	*143	*463			3,38
1894	2,638	*106	*143	*463			4,05
1895	1,344	*106	*143	*463			2,06
1896	2,070	*106	366	*463			3,18
1897	1,635	*106	22	*463			2,51
1898	965	*106	30	*463			1,48
1899	830	*106	155	*463			1,27
1900	2,074	*106	143	700			3,19
1901	3,629	*106	*100	*450			5,58
1902	2,715	*106	*100	*360			4,17
1903	1,064	*106	*50	*250			1,63
1904	1,639	246	82	167			2,52
1905	1,788	81	2	59			2,75
1906	3,414	35	34	163			5,25
1907	2,930	82	103	312		30	4,50
1908	1,608	86	126	286		7	2,47
1909	924	29	226	201		63	1,42
1910	1,493	47	129	99		43	2,29
1911	1,723	27	133	177			2,65
1912	1,245	6	74	413		29	1,91
1913	868	1	48	293		42	1,33
1914	540	10	56	143		60	83
1915	828	11	24	212	20	42	1,27
1916	2,232	1	15	215	**4	4	3,43
1917	2,350	4	8	222	**0	12	3,61
1918	1,120		2	147	**0	14	1,72
1919	1,105	2	5	80	**1	23	1,70
1920	1,371	1	5	15	2	11	2,10
1921	1,642	1		29	3	77	3,14
1922	658			12	2	17	1,05
1923	728		7	(5)	2	69	1,42
1924	891		4			35	1,95
1925	1,319	6	5		1	28	2,94
1926	2,384	[4] 3	74		2	102	4,91
1927	775	0	**12		**4	**15	1,64
1928	1,198		**9		**11	**3	2,29
1929	381		**57		**9	**21	1,28
1930	238		**21		**2	**18	1,32
1931	867		**20		**5	**5	1,74
1932	771		**39		**17	**7	1,50
1933	1,143		**30		**24	**11	2,11
1934	1,399		**57		**26	**15	2,84
1935	944		**26	337	**37	**21	1,82
1936	1,078		(6)	743	(6)	(6)	2,45
1937	1,071			255			2,33
1938	984			232			2,21
1939	509			174			1,21
1940	452			145			1,26
1941	697			222			1,62
1942	507			220			1,13
1943	806			450			1,72
1944	641			762			1,41
1945	676			659			1,33
1946	228			215			67
1947	110			156			59
1948	657			189			1,41
1949	450			55			1,14
1950	504			145			1,26
1951	149			60			82
1952	219			12			77
1953	77			47			81

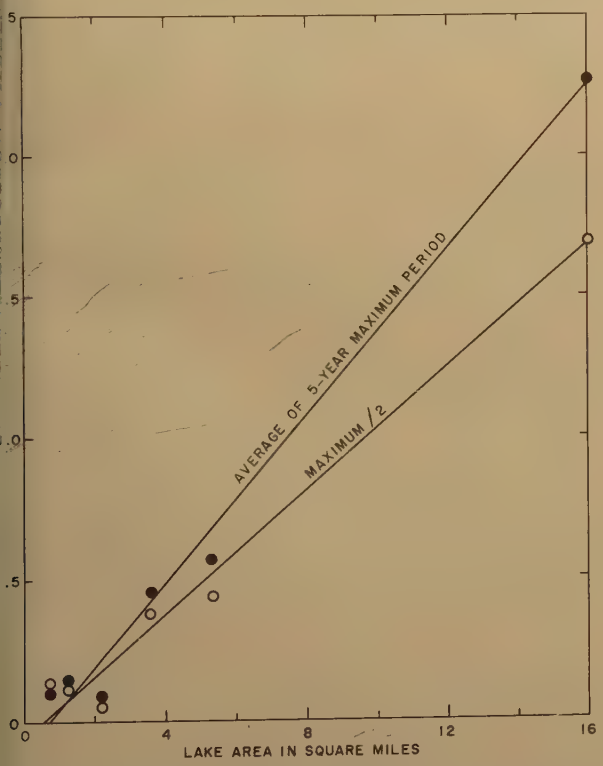
[1] Adjusted for estimated catches of other rivers included in Karluk figures
[2] 1888–1920 equals catch times 1.5385, 1921 and subsequently equals catch plus escapement.
[3] Most of area 2 in Afognak Reservation, no legal fishing 1892–1911.
[4] Area 5 assigned to Karluk catch 1926 and subsequently, except for Rich and Ball figures for 1926 and 1927.
[5] Area 9 closed 1923–1934.
[6] Subsequent to 1935 not available.
*=Estimated catch.
**=Catch minus trap catch.

id their relative productivity. The only other ckeye lake of any size on the islands is Afognak ake (approximate area of 2.8 square miles, water-ed of 32.5 square miles). Thus Karluk Lake is an area about equal to all of the other sockeye lakes on Kodiak and Afognak Island (there are very small lakes with small sockeye runs at several other points in addition to those listed in table 3, e. g., Buskin River, Eagle River, and Kizhuyak Bay).

ABLE 3.—*Lake areas of principal Kodiak Island sockeye streams adjacent to Karluk and their relative productivity since 1903* [1]

Source of water		Area in square miles [2]	Best 5 years	Average catch	Maximum catch any year since 1903	Year of maximum catch
rluk River	Karluk Lake	15.26				
	Thumb Lake	.31				
	O'Malley Lake	.47				
Total (Karluk River)		16.04	1904–08	2,269,562	3,382,913	1906
ttle River	Little Lake	.78	1904–08	105,850	246,131	1904
anik River	Uganik Lake	1.25	1907–11	143,436	226,477	1909
d River	Red Lake	3.27				
	Other lakes	.32				
Total (Red River)		3.59	1941–45	462,772	762,084	1944
nnery Stream	Akalura Lake	2.18	1917–21	[3] 91,899	[3] 103,777	1917
ga Creek	Olga lakes	5.29	1917–21	[3] 571,612	[3] 871,723	1917

[1] Before 1904 the records of catches by streams are incomplete.
[2] Planimeter measurement from Geological Survey Topographic Maps, Scale 1: 250,000.
[3] Weir counts, 1923–32, 1937–42 and 1944–51 showed Olga Creek with 6.22 times Cannery Stream so catch was allocated on that basis.



IGURE 3.—Relation between lake area and potential size of population.

Figure 3 shows that there is a close correspondence between lake area and potential production of sockeye in this general region. A 5-year average was used in order to discount short-term fluctuations in abundance, and since 5 is the dominant age at maturity in this region the use of a 5-year period is indicated. Prior to 1904 the allocation of catches to districts were available in part only, so earlier years were omitted in selecting the 5-year period of maximum catch. Of course the 5-year period selected is not the same for every stream since some streams were depleted during periods when others were not.

For this report, we have tentatively accepted the catch figures for Karluk presented in table 2. It will be noted that previous to 1903 the figures for Karluk production are slightly less than any previously used as we have subtracted the estimated catches for Little River, Uganik River, and Red River, which were included in published totals for Karluk in some of the years.

Comparison of abundance fluctuations in different lake

In determining the cause of the changes in abundance of the Karluk sockeye population it is

important to know whether these fluctuations are confined to Karluk only, or whether they have occurred simultaneously in other populations in the region. In table 4 are shown the total runs for Karluk and Red Rivers, and the weir counts in the Uganik River, Cannery Stream (Akalura Lake), and Olga Creek. For each locality the measure of the run that has been employed has been weighted to make its sum for the period of years available equal to the sum of the total Karluk run for the corresponding period of years. The plotted curves of figure 4 show that the five runs tend to fluctuate together, but the Uganik River series is too short to permit an adequate test of its significance.

For the other four streams the weighted total runs (or weir counts), columns 2 to 5, table 4, have been compared with one another with the following results:

Correlations between runs of sockeye, r

Streams	Cannery Stream	Red River	Karluk River
Olga Creek	.615**	.331	.781**
Cannery Stream		.689**	.506**
Red River			.672**

r^2

Olga Creek	.38	.11	.61
Cannery Stream		.48	.26
Red River			.45

Nearest airline mileage between lakes

Olga Creek	8	11	15
Cannery Stream		1	9
Red River			10

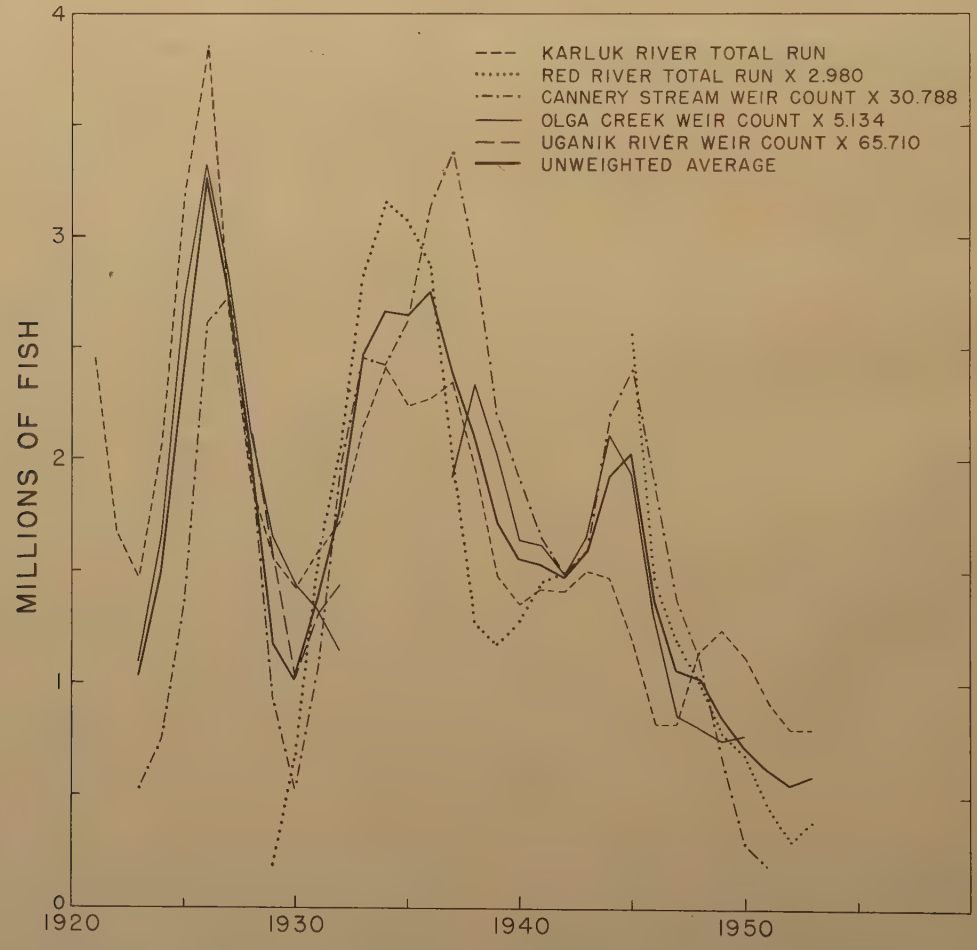


FIGURE 4.—Long-term fluctuations in the runs for Karluk River and other streams in the vicinity, all weighted to equal Karluk for same period of years with available data.

TABLE 4.—*Comparison of Kodiak Island sockeye salmon runs* [1]

[In thousands]

Year	Uganik: weir count	Karluk: total run	Red River: total run	Olga Bay		Trends [2]					Total		
				Cannery Stream: weir count	Olga Creek: weir count								
	A	B	C	D	E	A	B	C	D	E	Sum	Items	Average
1		3,142					2,447				2,447	1	2,447
2		1,058					1,670				1,670	1	1,670
3		1,423		493	863		1,465		534	1,092	3,091	3	1,030
4		1,954		616	1,550		2,068		747	1,645	4,460	3	1,487
5		2,940		1,262	2,618		3,188		1,343	2,710	7,241	3	2,414
6		4,918		3,233	4,056		3,856		2,609	3,322	9,787	3	3,262
7		1,647		2,709	2,557		2,626		2,725	2,833	8,184	3	2,728
8	2,366	2,292		2,248	2,161	2,125	1,878		1,940	2,109	8,052	4	2,013
9	1,643	1,282	86	554	1,556	1,577	1,548	190	916	1,651	5,882	5	1,176
0	657	1,325	399	308	1,330	1,018	1,418	682	516	1,436	5,070	5	1,014
1	1,117	1,740	1,842	893	1,530	1,314	1,578	1,566	1,047	1,332	6,837	5	1,367
2	2,366	1,509	2,181	2,094	940	1,940	1,717	2,068	1,963	1,137	8,825	5	1,765
3		2,111		2,771			2,145	2,818	2,448		7,411	3	2,470
4		2,849	3,454	2,155			2,407	3,152	2,424		7,983	3	2,661
5		1,820	2,548	2,617			2,236	3,058	2,617		7,911	3	2,637
6		2,453	3,680	3,079			2,266	2,856	3,125		8,247	3	2,749
7		2,336	1,517	3,725	1,299		2,335	1,990	3,379	1,920	9,624	4	2,406
8		2,214	1,246	2,986	3,163		1,945	1,269	2,878	2,338	8,430	4	2,108
9		1,215	1,067	1,816	1,725		1,478	1,165	2,201	2,030	6,874	4	1,718
0		1,268	1,281	2,186	1,509		1,345	1,282	1,909	1,643	6,179	4	1,545
1		1,629	1,499	1,447	1,828		1,418	1,446	1,647	1,622	6,133	4	1,533
2		1,136	1,505	1,509	1,325		1,407	1,503	1,488	1,493	5,891	4	1,473
3		1,727					1,500		1,601	1,656	4,757	3	1,586
4		1,410		1,693	1,987		1,470		2,206	2,117	5,793	3	1,931
5		1,335	3,239	3,233	2,377		1,188	2,573	2,409	1,936	8,106	4	2,026
6		670	1,240	1,478	1,001		818	1,470	1,894	1,295	5,477	4	1,369
7		595	1,162	1,385	801		818	1,194	1,370	859	4,241	4	1,060
8		1,410	1,213	1,232	832		1,139	1,013	1,116	813	4,081	4	1,020
9		1,141	465	616	786		1,239	775	662	751	3,427	4	857
0		1,263	957	185	601		1,122	684	293	766	2,865	4	716
1		822	355	185	1,078		920	458	185	919	2,482	4	620
2		774	167				795	297			1,092	2	546
3		811	498				799	388			1,187	2	594
eight factor	65.710	0	2.980	30.788	5.134								

[1] All runs weighted so that sums of years correspond to same years at Karluk.
[2] Smoothed once by 3's, with double weight on center item.

Out of 6 comparisons, all but 1 were highly gnificant. The coefficient of determination, r^2, aries in the other 5 comparisons from .26 to .61 nowing that the fluctuations in the runs are to a nsiderable extent controlled by elements common o all.

Although the sea-distance between the mouths f the streams issuing from these lakes varies om about 7 to 75 miles, the lakes lie in a com-aratively small area, the greatest distance be-ween any two of them being 15 miles in a direct ne. Because they lie in such a small area it is bvious that any major climatic changes must ffect them all in the same direction. Clearly, nen, we must begin by examining the climatic actors.

FFECTS OF CLIMATE ON SUCCESS OF REPRODUCTION

The measurement of the effect of climate on the uccess of reproduction is important from two tandpoints. If any one of the climatic factors which have a significant influence show a long-term trend it could conceivably be an important cause of long-term abundance trends. Furthermore, short-term changes in abundance caused by climatic factors serve to obscure the effect of other factors by causing excessive variation in the data. Aside then from the intrinsic value of knowledge of the effect of climatic factors, it is highly desirable to measure their effect so that they may be discounted in further analysis of the abundance data.

In examining the relations between success of survival and the physical environment, we were unable to avail ourselves of the advantages of multiple regression because the different series of data on the ecological factors are not equal, either in number or in specific years represented. The ecological factors have, therefore, been considered one by one. By so doing one loses the effect of interaction between factors. Also, one cannot always be certain of the amount of variation caused by any one factor. For instance, a factor

may not show any significant correlation with survival. However, if this same factor be again related to survival, after the effects of some other factor have been removed, the relation may be statistically significant. By this method of successive elimination it is possible to underestimate the total effect of the factors considered.

We have considered only those elements of the climate for which sufficient records exist and which can logically affect survival or growth at some stage of the salmon's existence. The factors considered were examined only in the order in which they are presented in the text. The factors examined are presented in table 5. The validity of the use of Kodiak air temperatures as representative of the Karluk Lake water temperatures was carefully examined (see appendix I) and verified.

In order to relate these climatic factors to survival it was necessary to have a measure of the success of each season's spawning in terms of survival. The total run (table 2) could not be used directly because the size of the population changed with time. It was, therefore, necessary to use not the run but the size of the returning population in relation to the number of spawners that produced it (table 6). The details concerning the derivation of the escapement and return figures of table 6 are developed in appendix D.

Examination of the data in table 6 reveals that the return per spawner cannot be used directly as a measure of spawning success since the return per spawner is correlated with the number of spawners. The regression of returns on number of spawners is shown in figure 5. The data divide rather sharply into two periods, the break occurring between 1923 and 1924. The relation is not strictly linear, as is illustrated in figure 5 by plots of group averages and empirical curves.

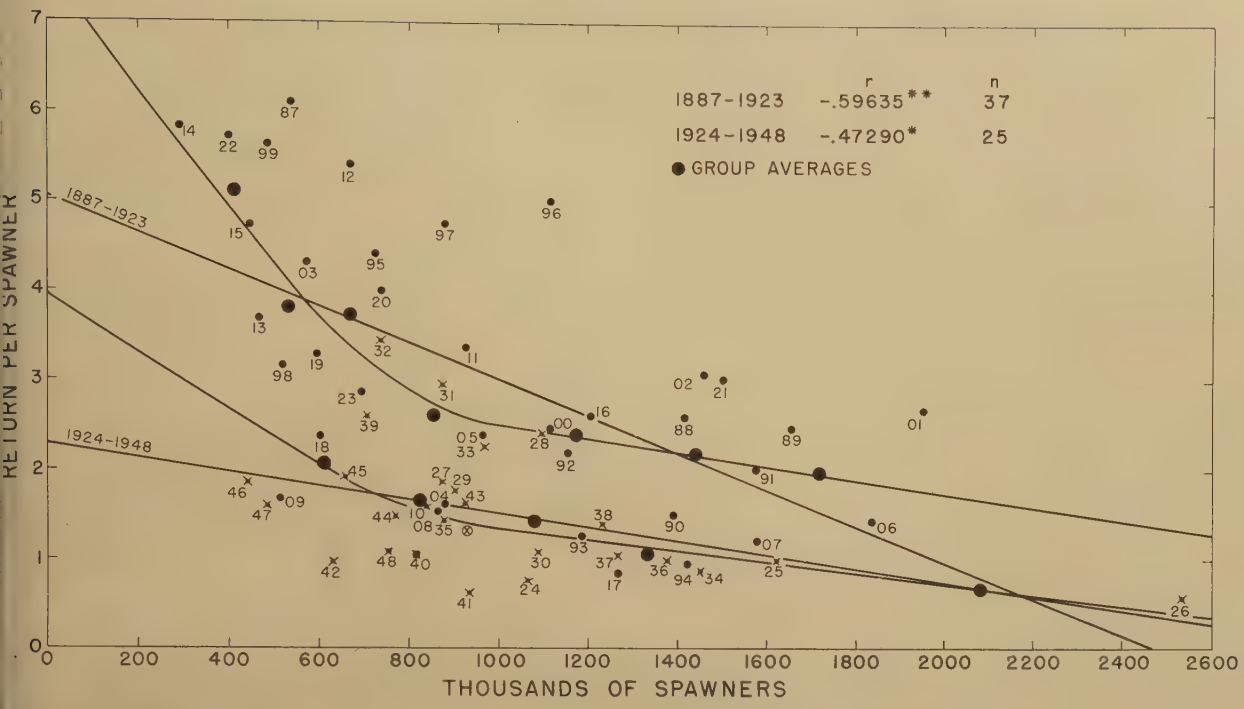
Enactment in 1924 of the White Act empowered the Secretary of Commerce (now Interior) to require a minimum escapement of 50 percent of the run. Thus 1924 became the first season in which the size of the escapement was regulated. Thus there is a natural break between 1923 and 1924, the latter period representing regulated escapements opposed to the chance escapements of earlier years.

In order to obtain a linear relationship the number of spawners was transformed into logarithms. The regressions of return per spawner on the logarithm of the number of spawners are shown in figures 6 and 7 for the early and recent periods. The reason for the considerable fall in the return per spawner after 1923 is not apparent in these data, but as we shall show later may perhaps be linked with some change in the

TABLE 5.—*Certain climatic factors for Kodiak, Alaska*

Year	Average monthly temperatures °F		Accumulated monthly temperature 45° to 55°F including previous year	Average precipitation April to July in inches
	April–May	October–December		
1869	42.55	38.17		22.78
1870	39.05			12.63
1881				
1882				22.05
1883				28.01
1884				13.50
1885				19.77
1886				11.40
1887				27.22
1888				14.56
1889				20.16
1890				16.77
1895		[2] 42.22		
1896	35.30			
1897				
1898		[2] 39.78		
1899	40.10	[2] 38.98		10.80
1900	41.30	[2] 31.75		19.21
1901	39.70	37.63		
1902	42.25			12.23
1903	40.70	36.33		21.71
1904	41.20	36.57	62.7	10.65
1905	44.25	[2] 37.92		9.60
1906	41.50	37.03		
1907	41.65	34.70		15.61
1908	37.30		45.4	19.19
1909	38.05	[2] 31.23	36.0	20.55
1910	35.70	33.33		20.85
1911	35.45	35.30		16.80
1912				
1913		35.20		18.01
1914	41.00	38.30		23.93
1915	[1] 43.30	35.00		
1916	38.60	31.17	55.1	22.87
1917	39.40	30.27	38.8	15.02
1918			49.2	6.29
1919	39.10	36.00	57.6	20.81
1920	37.15	35.13	48.3	13.57
1921	39.10	37.67	42.4	15.27
1922	38.40	36.77	52.0	15.41
1923	40.55	37.47	57.1	12.79
1924	38.40	37.10	59.7	8.67
1925	38.05	38.07	61.8	13.92
1926	42.50	39.83	71.6	18.01
1927	38.55	33.37	57.6	23.24
1928	39.00	37.60	40.3	21.20
1929	40.80	39.17	57.0	18.28
1930	39.60	36.83	59.9	15.30
1931	41.90	36.97	54.0	16.83
1932	40.70	36.53	51.4	23.70
1933	40.20	34.93	47.4	17.23
1934	40.90	37.80	53.7	21.65
1935	41.80	37.70	59.7	22.60
1936	40.65	38.60	67.9	11.57
1937	40.50	38.60	57.8	26.99
1938	40.60	38.57	44.4	35.24
1939	39.60	34.97	50.2	14.14
1940	43.60	39.27	55.1	25.19
1941		36.07		21.65
1942	44.00	32.03		
1943	40.00	37.33	62.6	
1944	38.90	37.27	56.3	
1945	[1] 39.10	31.83	56.0	
1946	[1] 39.30	34.80	53.1	
1947	39.30	37.07	54.6	
1948	41.60	32.50	49.5	
1949	37.95	36.43	48.3	
1950	38.30	34.07	49.2	
1951	39.30	36.17	50.1	
1952	37.45	37.33	51.6	
1953	40.05	35.97	57.5	

[1] Based on 1 month's record.
[2] Based on 2 months' records.



IGURE 5.—Relation between return per spawner and number of spawners (escapement). This shows both least square curves and empirical curves from grouped averages to illustrate the curvilinearity of the plots.

ABLE 6.—*Showing the number of spawners and the resulting runs from 1887 to 1948*

[In thousands]

ear of awning	Escapement [1] (spawners)	Returns [2] (progeny)	Returns per spawner	Year of spawning	Escapement [1] (spawners)	Returns [2] (progeny)	Returns per spawner
87	541	3,292	6.09	1921	1,500	4,494	3.00
88	1,417	3,382	2.39	1922	400	2,282	5.71
89	1,646	4,059	2.47	1923	695	1,990	2.86
90	1,389	2,068	1.49	1924	1,063	809	.76
91	1,579	3,185	2.02	1925	1,621	1,607	.99
92	1,152	2,515	2.18	1926	2,534	1,461	.58
93	1,184	1,485	1.25	1927	872	1,618	1.86
94	1,421	1,277	.90	1928	1,094	2,630	2.40
95	724	3,191	4.41	1929	901	1,587	1.76
96	1,115	5,583	5.01	1930	1,087	1,172	1.08
97	880	4,177	4.75	1931	873	2,578	2.95
98	520	1,637	3.15	1932	738	2,538	3.44
99	447	2,522	5.64	1933	968	2,186	2.26
00	1,117	2,751	2.46	1934	1,450	1,261	.87
01	1,954	5,252	2.69	1935	876	1,250	1.43
02	1,462	4,508	3.08	1936	1,375	1,353	.98
03	573	2,474	4.32	1937	1,265	1,334	1.05
04	883	1,422	1.61	1938	1,230	1,587	1.29
05	963	2,297	2.39	1939	706	1,831	2.59
06	1,838	2,651	1.44	1940	816	858	1.05
07	1,578	1,915	1.21	1941	932	575	.62
08	866	1,335	1.54	1942	629	607	.97
09	498	831	1.67	1943	921	1,495	1.62
10	804	1,274	1.58	1944	769	1,141	1.48
11	928	3,434	3.70	1945	659	1,263	1.92
12	670	3,615	5.40	1946	442	822	1.86
13	467	1,723	3.69	1947	485	774	1.60
14	291	1,700	5.84	1948	754	811	1.08
15	446	2,109	4.73	1949	691		
16	1,202	3,142	2.61	1950	759		
17	1,265	1,058	.84	1951	673		
18	603	1,423	2.36	1952	556		
19	595	1,954	3.28	1953	734		
20	738	2,940	3.98				

[2] Prior to 1921 equals catch times 0.5385 (35/65).
[1] 1921–48 based on actual returns, other years equals catch and escapement years later.

seasonal distribution and variation in size of the escapements.

The residuals (table 7) of the return per spawner on $\log_{10}$ number of spawners (plus or minus deviations of the return per spawner from the regression line) were derived from the regression curves of figures 6 and 7. These residuals, plotted in figure 8, show long-term fluctuations that could scarcely be considered random.

If we let y equal returns and x equal number of spawners, the formula used in fitting these regressions is $\log y = x\epsilon^{a-b \log x}$ which can also be written as $y=(a-b \log x)x$ (see plot of x and y values in fig. 19). For purposes of fitting it was more convenient to use the straight line form of the equation $y/x=a-b \log x$. A comparison of this and an alternative method of deriving residuals of return on escapement is given in appendix H.

The use of the residuals of the return per spawner on the logarithm of the number of spawners for comparison with climatic effects removes the necessity for an extremely complex analysis in which allowances would have to be made both for actual abundance of the parent broods and for long-term trends in the abundance

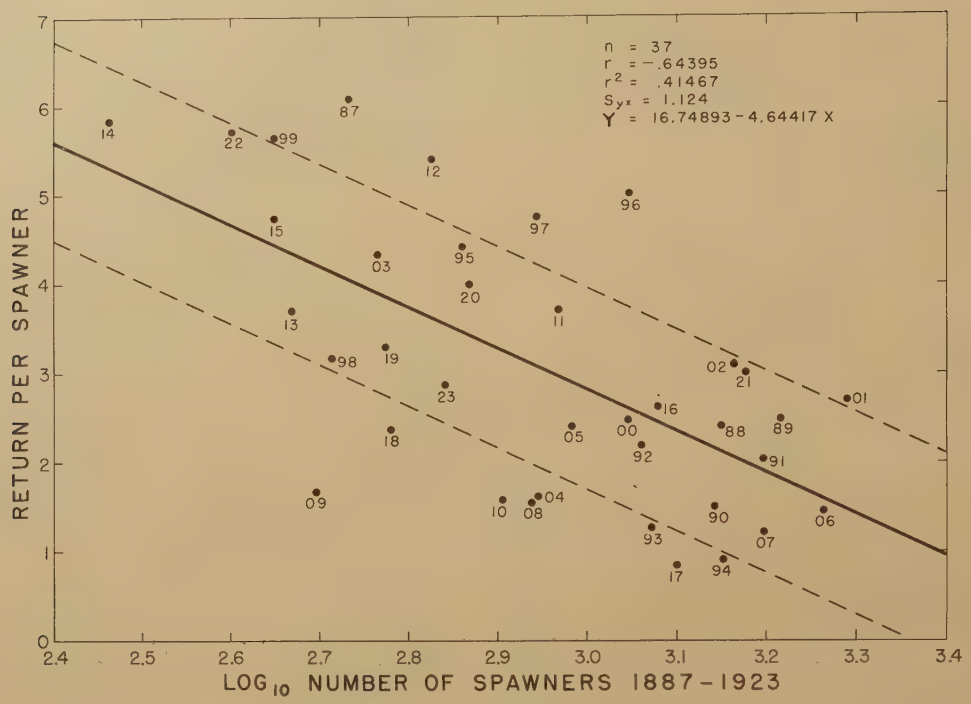


FIGURE 6.—Regression of return per spawner on log number of spawners, 1887 to 1923.

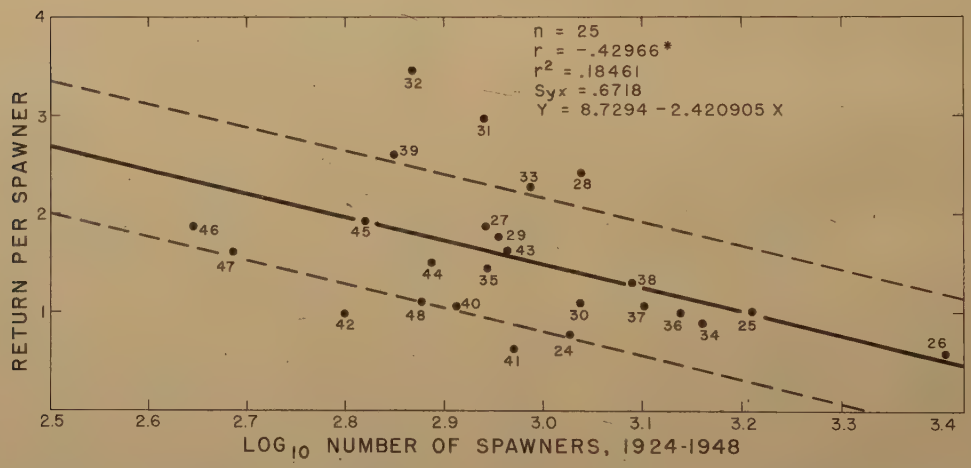


FIGURE 7.—Regression of return per spawner on log number of spawners, 1924 to 1948.

of the runs. In table 7 (column 2) the residuals are shown as "residuals plus three" as a matter of convenience to give all the residuals a positive value, obviating the inconvenience of working with plus and minus values.

In the following sections the comparison of these residuals with climatic factors is explained, and the corrections shown in columns 3, 4, 5, and 7 of table 7 are derived.

Effect of autumn temperatures on survival of eggs

There is evidence for other species of *Oncorhynchus* that there may be a relation between autumn temperatures and survival. Thus in southeastern Alaska experiments on the pink salmon (*O.*

TABLE 7.—*Residuals of return per spawner on $\log_{10}$ number of spawners corrected for ecological factors*

Year of spawning	Residuals (plus three)	Corrections to residuals for temperature factors			Residuals corrected for temperature factors	Correction for April–July rainfall (inches)	Residuals corrected for all physical factors
		October–December °F	Accumulated °F	April–May °F			
37	5.02				5.02	−.28	4.74
38	3.28				3.28	−.11	3.17
39	3.67				3.67	−.49	3.18
40	2.35				2.35		2.35
41	3.13				3.13		3.13
42	2.65				2.65		2.65
43	1.79				1.79		1.79
44	1.82				1.82		1.82
45	3.93	0		1.23	5.16		5.16
46	5.40				5.40		5.40
47	4.66				4.66		4.66
48	2.02	0		−.34	1.68	.41	2.09
49	4.19	0		−.30	3.89	−.16	3.73
50	2.87	.78		−.22	3.43		3.43
51	4.23	0		−.05	4.18	.12	4.30
52	4.03		.02	−.40	3.65	−.02	3.63
53	3.41	0		−.33	3.08	.39	3.47
54	1.55	0		.46	2.01	.56	2.57
55	2.50	0		−.25	2.25		2.25
56	2.85	0	.04	−.21	2.68	−.36	2.32
57	2.33	.11	.51	.57	3.52	−.16	3.36
58	1.45			.39	1.84	−.08	1.76
59	.45	.89		1.09	2.43	−.07	2.36
60	1.33	.42		1.17	2.92	−.31	2.61
61	3.74	0			3.74		3.74
62	4.77				4.77	−.23	4.54
63	2.35	0		−.36	1.99	.12	2.11
64	3.53	0	−.15	.22	3.60		3.60
65	3.28	0	.58	.14	4.00	.05	4.05
66	3.17	1.00	−.03	−.12	4.02	−.34	3.68
67	1.51	1.13	−.15		2.49	1.14	3.63
68	1.53		0	−.03	1.50	−.07	1.43
69	2.41	0	.21	.61	3.23	−.10	3.13
70	3.55	0	−.10	−.03	3.42	−.35	3.07
71	4.01	0	−.15	.20	4.06	−.36	3.70
72	4.04	0	−.10	−.40	3.54	.02	3.56
73	2.31	0	−.02	.20	2.49	.73	3.22
74	2.36	0	.73	.32	3.41	−.16	3.25
75	3.03	0	−.15	.01	2.89	−.23	2.66
76	3.08	0	.31	.15	3.54	.08	3.62
77	3.24	.57	−.15	.01	3.67	−.05	3.62
78	4.02	0	−.09	−.39	3.54	−.21	3.33
79	3.17	0	−.13	−.18	2.86	−.36	2.50
80	2.70	0	−.08	−.15	2.47	−.31	2.16
81	4.33	0	.03	−.40	3.96	.10	4.06
82	4.65	0	−.13	−.36	4.16	−.28	3.88
83	3.95	0	−.10	−.38	3.47	−.02	3.45
84	2.79	0	.42	−.17	3.04	.04	3.08
85	2.83	0	−.15	−.40	2.28	.23	2.51
86	2.85	0	.14	−.40	2.59	.29	2.88
87	2.83	0	−.05	−.40	2.38	.79	3.17
88	3.04	0	−.15	−.18	2.71	−.21	2.50
89	3.75	0		.30	4.05	.19	4.24
90	2.37	0			2.37	−.02	2.35
91	2.07	0	0	.40	2.47		2.47
92	2.01	.72	−.16	−.32	2.25		2.25
93	3.06	0	−.15	.05	2.96		2.96
94	2.74	0	−.12	.05	2.67		2.67
95	3.01	.76	−.15	−.08	3.54		3.54
96	2.53	.09	−.04	−.08	2.50		2.50
97	2.38	0	0	−.22	2.16		2.16
98	2.32	.76	−.03	.36	3.41		3.41

orbuscha) are highly suggestive. Hanavan and kud (1954) state concerning survival of young rom known numbers of spawners:

> The interplay of natural and imposed conditions on the ntertidal experiments for the years 1949, 1950, and 1951 esulted in survival rates of 20.9, 3.2, and 19.8 percent in ens that contained 3 females located at the 8- and 9-foot ide levels. Survival rates in Sashin Creek for these years ere 3.7, 0.1, and 9.3 percent. The average for the 12-year eriod 1940–51 was 2.54 percent. The similarity in the ears of occurrence of the high- and low-survival rates in he intertidal and fresh-water areas suggests a response to common environmental factors and specifically to those factors related to the fresh-water environment.

It may be significant in this regard that the winter of 1950–51 was unusually cold with the greatest departure from normal temperatures occurring in November. In the 12-year period 1940–51, the four lowest survival rates in Sashin Creek coincided with the four coldest Novembers suggesting that abnormally low stream temperatures occurring early in the incubation period (between the 6th and 10th weeks) may be particularly damaging to the developing eggs. The average Sashin Creek stream temperature for November in 1949 was 43.3° F., in 1950 it was 36.9° F., and in 1951 it was 39.4° F.

There is also evidence for the Columbia River chinook salmon (*O. tshawytscha*) that winter temperatures subsequent to spawning have an effect on survival as measured by ultimate returns of adult salmon (Silliman 1950). For an 11-year period he obtained a correlation coefficient of 0.337 between survival and the overall range of temperatures which compares closely with 0.363 (significant) for Karluk. Although this series of years was too short to permit detailed analysis, he suggests that the relationship should logically be curvilinear since once winters are warm enough to avoid freezing of eggs, little or no improvement can be expected from further increases in temperature.

In table 5 are presented average monthly air temperatures (see appendix I for the relation between Kodiak air temperatures and Karluk Lake water temperatures) at Kodiak for two periods of months, (1) October to December, (2) April and May. The same table also includes the accumulated monthly average degrees of temperature by 2-year periods falling between 45° and 55° F., and the average monthly precipitation in inches from April to July, inclusive, for Kodiak.

The October–December temperatures are shown in figure 9. Long-term changes in the trend are clearly evident and there appear to be short-term fluctuations also. The feature of chief interest to this study is the pronounced difference in the level of the trend during different periods of years, e. g., from 34° F. in the years close to 1913 to over 37° F. from 1924 to 1938. A difference of 3° F. during the period soon after spawning, while the eggs are still in a very sensitive stage, could have a marked effect on survival.

The regression of the residuals (of return per spawner on $\log_{10}$ number of spawners) on the October to December average temperature is given in figure 10. Over the total range of tem-

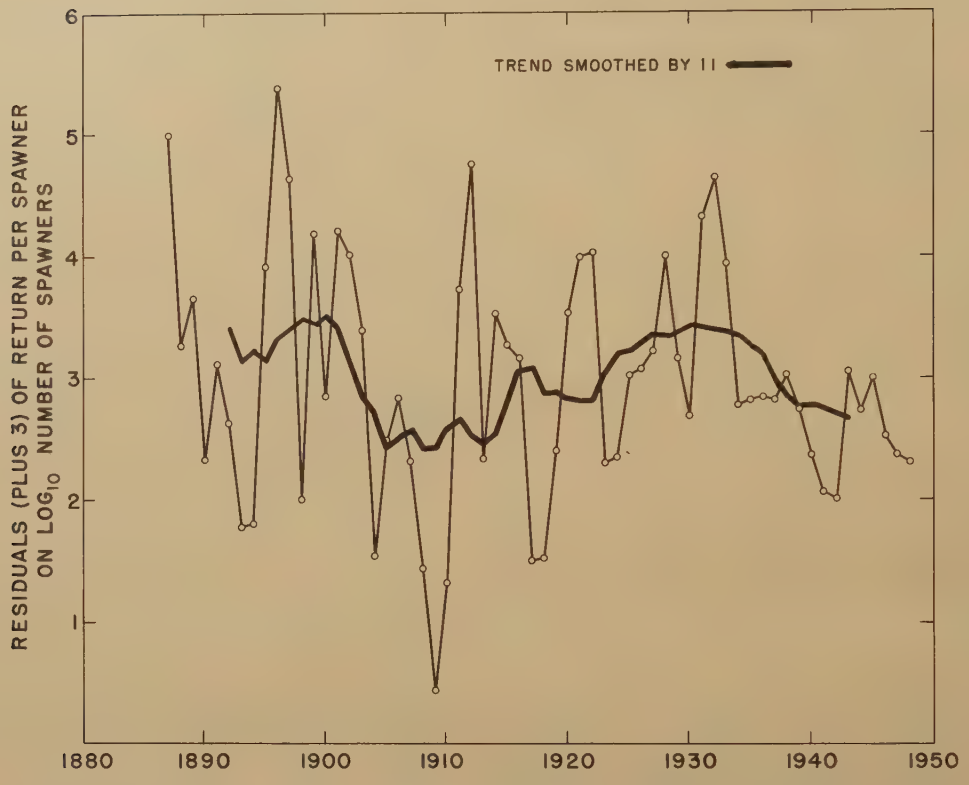


FIGURE 8.—Residuals of return per spawner on log number of spawners showing long-term trends.

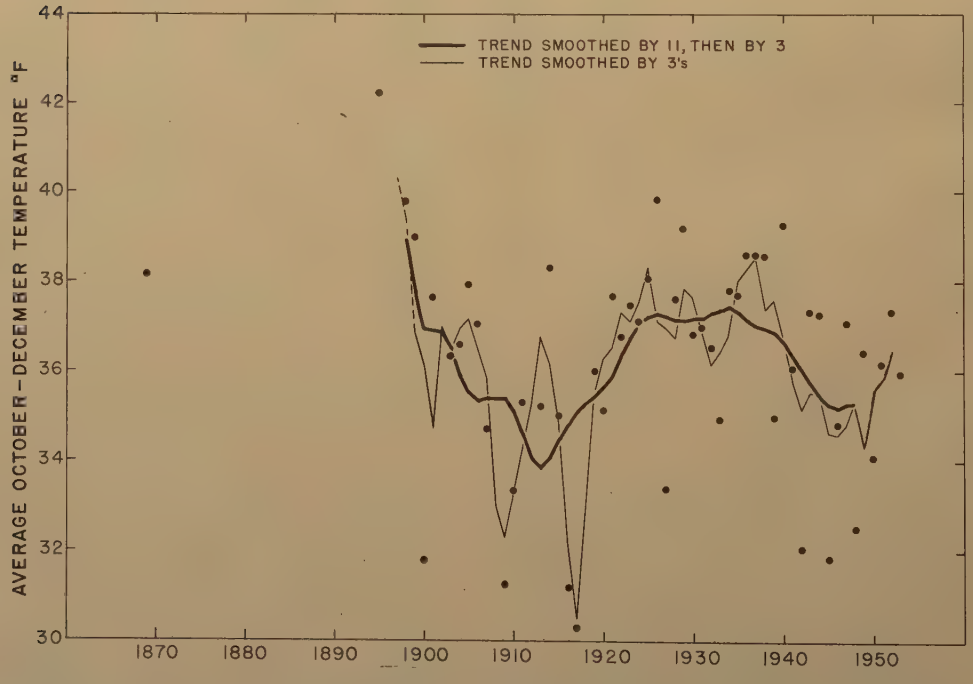


FIGURE 9.—Annual and smoothed trends of air temperature for October to December, inclusive, at Kodiak.

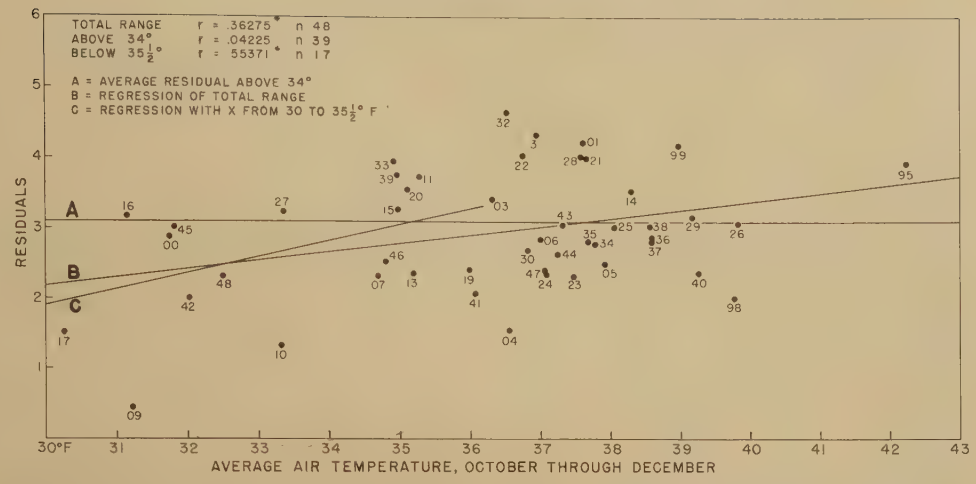


FIGURE 10.—Regression of residuals (Y) of return per spawner on log number of spawners on October–December average air temperature at Kodiak (X).

eratures the correlation is only 0.363, which, lthough statistically significant is rather low. nspection of figure 10 shows, however, that this s caused by a lack of any correlation at the igher temperatures. That is, October–December emperatures are a limiting factor on survival nly when they fall below a certain threshold. Thus above 34° F. the correlation is nonexistent 0.042), while from 30° to 35.5° the correlation s 0.554 and significant.

To allow for the effect of October–December emperatures the regression of the residuals (Y) n temperatures from 30 to 35.5 degrees has been lotted in figure 10 (curve C) and extended to ut curve A, which is the average of the residuals aving a temperature (X) above 34° F. All esiduals with an X below 35 degrees (34.9° or ower) were then corrected for autumn tempera- ure by adding the difference between curves A nd C. The net effect is that in 11 out of the 8 years with data the autumn temperatures were ufficiently low to affect survival of the eggs.

Effect of length of growing season on survival of young

The second factor considered was the effect of emperature on survival through its effect on rowth of the smolts. Since the desideratum vas a measure of the length of the growing sea- on, we have employed the accumulated average nonthly temperatures above 45° F., omitting for ny month any excess over 55° F. As the great najority of the smolts migrate to sea in their hird year (after spending two full summers in the lake) the accumulated temperatures for the two calendar years succeeding the year of spawning have been used (see table 5).

These accumulated temperatures are shown in figure 11 plotted against the residuals (corrected for the October–December temperature subsequent to spawning) for return per spawner against $\log_{10}$ number of spawners. Linear correlation throughout the range of accumulated temperatures is practically nonexistent (0.0144), but for the range of accumulated temperatures below 60° F. it is 0.385, and significant.

Obviously, y as a function of x is curvilinear. Note that the last 5 points out of 6 on the left and the last 4 points on the right fall below the average. The shape of the empirical curve shown was determined from the grouped averages.

The curvilinear correlation was determined from the deviations, z, of the individual y's from the empirical curve according to the formula:

$$\overline{P}^2_{yx}=1-\left(\frac{\sigma_z^2}{\sigma_y^2}\right)\left(\frac{n-1}{n-m}\right)$$ Ezekiel (1930),

where m was made to equal 3 on the assumption that the regression curve used could have been mathematically represented by an equation with three constants, such as a parabola.

Similarly the standard error of estimate was determined by the formula:

$$\overline{S}^2_{y\cdot f(x)}=\frac{n\sigma_z^2}{n-m}$$

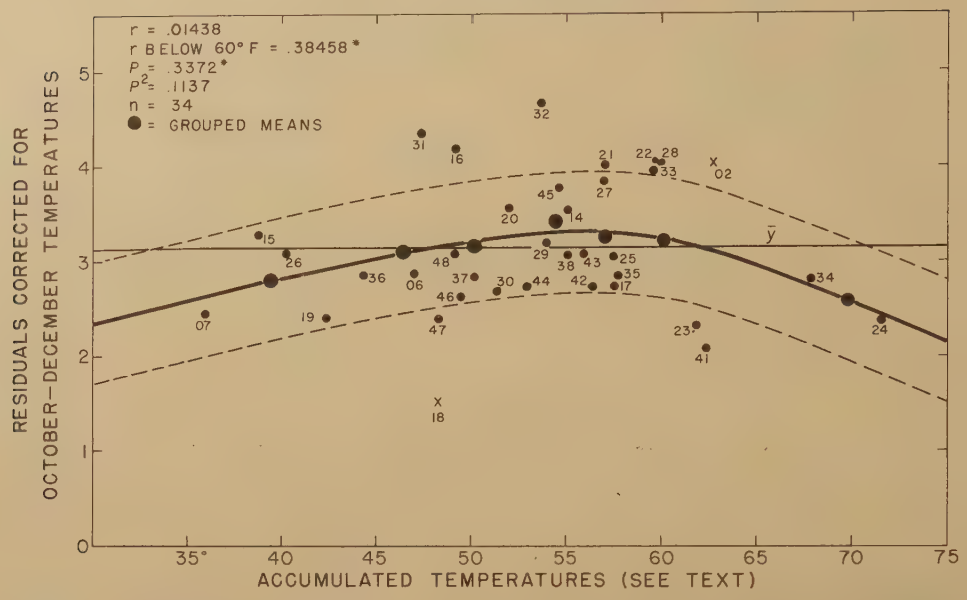


FIGURE 11.—Regression of residuals (see text) corrected for October–December temperature on the accumulated monthly temperatures between 45° and 55° F. for the two calendar years subsequent to year of spawning.

The index of correlation, P of 0.3372 has a probability of less than .05. The standard error of estimate of P is .6277.

The index of determination, P^2 is .1137, indicating that about 11 percent of the residual variation in y (variation remaining after correcting for the October–December temperatures) is associated with these accumulated temperatures.

The residuals of return per spawner on log number of spawners (corrected for the October–December temperatures) were now further corrected by adding the difference between the average Y and the fitted curve for each point. This correction eliminates the influence of the factor considered, at the same time keeping the years corrected on the same basis as those for which lack of data prevents correction for this particular factor.

Effect of spring temperatures on emergence of fry

The third factor to be considered was the spring temperature (April and May) for the year subsequent to spawning. These average temperatures are shown in figure 12 plotted against the residuals corrected as mentioned above. As with the first two factors the relationship is not linear and r is only 0.183 without significance

In the same manner as described above, P was determined to be 0.5203 with a P of less than .01. As for the other factors, the residuals were now corrected by adding the difference between the average Y and the fitted curve for each point. It is clear that the spring temperatures exert an influence on ultimate survival which we tentatively ascribe to an effect on the survival of the fry that are either emerging or about to emerge from the redds. The residuals corrected for all temperature factors are given in table 7.

Effect of rainfall on survival

In considering the possible role of precipitation it was expected that the summer rainfall might have a noticeable effect on ultimate survival through its effect on success of spawning. Figure 13 shows the residuals (corrected for the temperature factors) plotted against total rainfall from June to August. The linear coefficient of correlation is only 0.287 over the total range of rainfall, but there seems to be a tendency for the residuals to decrease with low rainfall. Below 13.5 inches of rain the coefficient of correlation increases to 0.388, but the available years are too few to establish statistical significance, as P is slightly larger than 0.05. Since definite statistical proof of a relationship could not be established no corrections for this factor were attempted.

Considering the widely held opinion that water levels during the spawning period are important to success of reproduction, the lack of correlation in these data is a little surprising. However, the lack of correlation may not be due to the lack

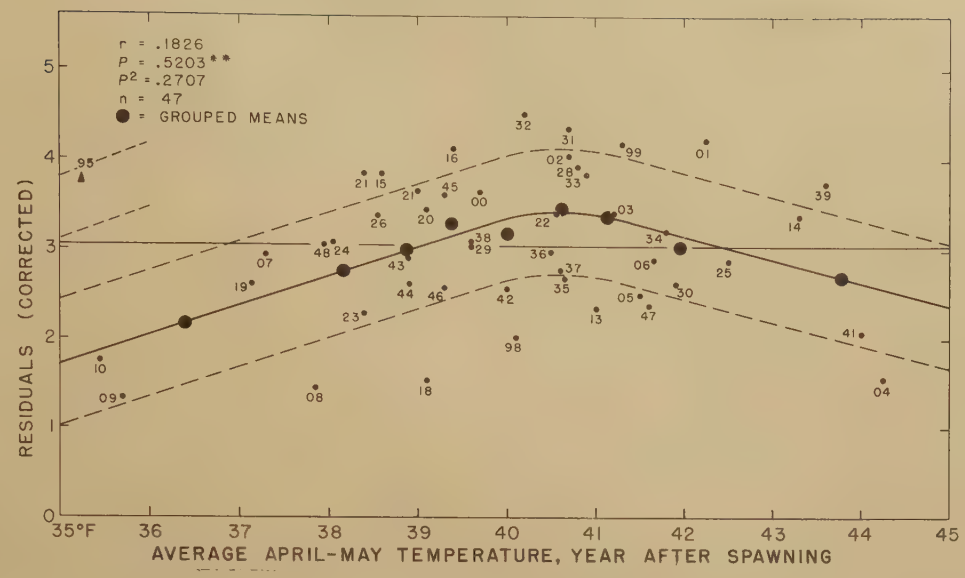


FIGURE 12.—Regression of corrected residuals on the average April–May air temperature at Kodiak.

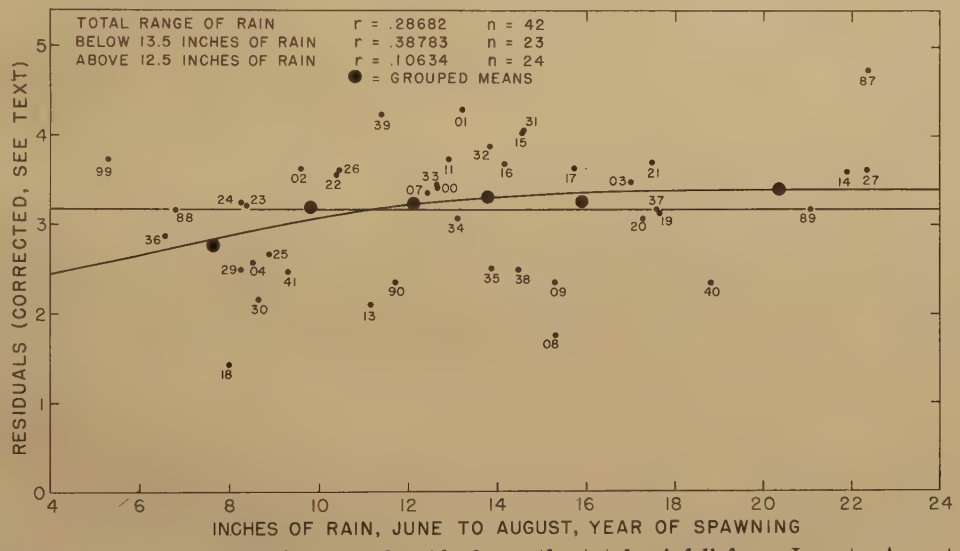


FIGURE 13.—Regression of corrected residuals on the total rainfall from June to August, inclusive, at Kodiak.

of effect of water levels on survival; rather, the lack of any significant correlation may be ascribed to the lack of a sufficiently accurate measure of rainfall at Karluk. In country as mountainous as Kodiak Island, with a high mountain barrier between the observation point at Kodiak and the point of reference, Karluk Lake, the Kodiak rainfall may not be sufficiently representative of Karluk rainfall.

That waterlevels during the spawning period can have a very marked effect on sockeye survival is indicated by the relationship between rainfall and spawning on the Skeena River (Brett 1951). An explanation of these Skeena River data is given in appendix E.

A relation was discovered between the residuals and the rainfall in spring and early summer of the year following spawning. Such a relationship has a logical explanation for this is the period during which the fry from the spawning of the previous autumn would normally be emerging from the redds, and dry streambeds, or floods, would certainly decrease their survival. As before, the correlation was not high, but this may also be related to the fact that the rainfall data may not be truly representative of actual precipitation.

The relation is shown graphically in figure 14. As is quite usual with this type of data linear correlation over the total range of rainfall in nonexistent, r is 0.039. However, below 16 inches of rainfall the correlation is 0.535 and significant. Above 15 inches of rain the correlation of −0.309 is not quite statistically significant. A slight minus correlation with higher rainfall would be a logical consequence as the emerging fry would be damaged by floods. Unfortunately, the data in hand for monthly rainfall at Kodiak do not reveal flood conditions at Karluk. The index of correlation for the empirical curves formed by joining the linear curves for the two segments of the range is 0.316 and significant.

The corrections for the residuals and the corrected residuals are given in table 7, and table 8 shows the return per spawner corrected for all the available physical factors.

TABLE 8.—*Return per spawner corrected for physcial factors*

Year	Corrected return per spawner	Number of factors corrected	Year	Corrected return per spawner	Number of factors corrected
1887	5.81	1	1918	2.26	
1888	2.28	1	1919	4.00	
1889	1.98	1	1920	3.50	
1890	1.49		1921	2.69	
1891	2.02		1922	5.23	
1892	2.18		1923	3.77	
1893	1.25		1924	1.65	
1894	.90		1925	.62	
1895	5.64	2	1926	1.12	
1896	5.01		1927	2.24	
1897	4.75		1928	1.71	
1898	3.22	3	1929	1.09	
1899	5.18	3	1930	.54	
1900	3.02	2	1931	2.68	
1901	2.76	3	1932	2.67	
1902	2.72	3	1933	1.76	
1903	4.38	3	1934	1.16	
1904	2.63	3	1935	1.11	
1905	2.14	2	1936	1.01	
1906	.91	4	1937	1.39	
1907	2.24	4	1938	.75	
1908	1.85	2	1939	3.08	
1909	3.58	3	1940	1.03	
1910	2.86	3	1941	1.02	
1911	3.70	1	1942	1.21	
1912	5.17	1	1943	1.52	
1913	3.45	3	1944	1.41	
1914	5.91	3	1945	2.45	
1915	5.50	4	1946	1.83	
1916	3.12	4	1947	1.38	
1917	2.96	3	1948	2.17	

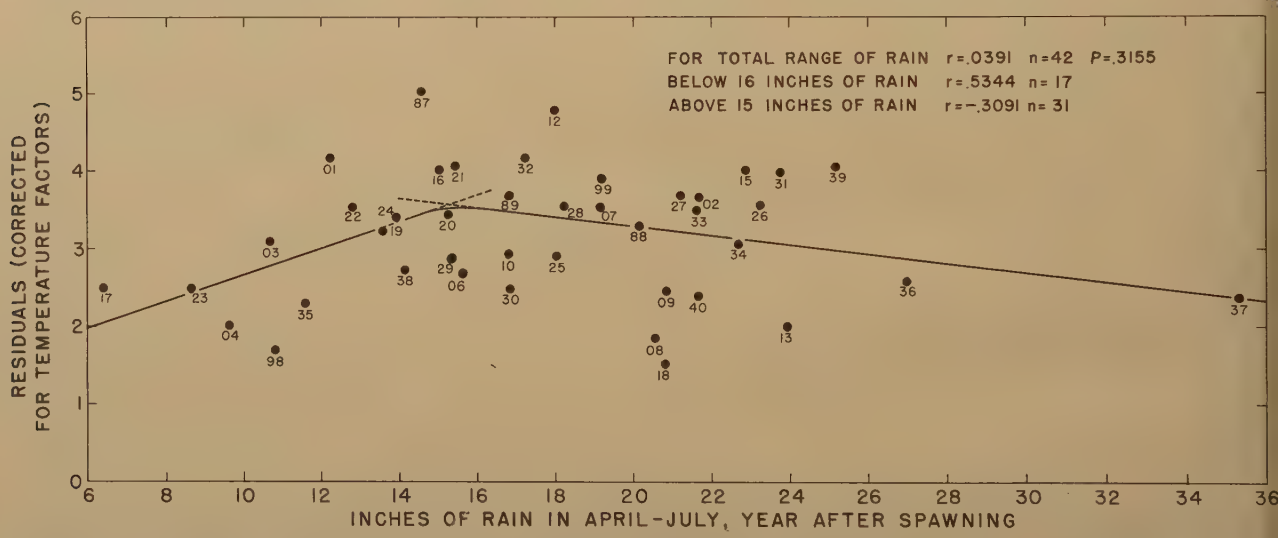


FIGURE 14.—Regression of corrected residuals on the total rainfall from April to July, inclusive, at Kodiak in the year subsequent to spawning.

SOCKEYE ABUNDANCE IN THE ODD- AND EVEN-NUMBERED YEARS

It has long been conceded that the runs of pink salmon to the Karluk River can be detrimental to successful reproduction of the sockeye. It has been generally held that this detrimental effect is confined to the occasional year when the predominant even-year population of pink salmon reaches a peak so that large numbers overflow from their normal spawning beds in the main river below the lake. Entering the lake they then ascend the tributary streams and compete with the sockeye for the limited spawning gravels.

Such a straightforward explanation while having the merit of simplicity does not explain all the facts. If we first examine the records for the pink salmon, we find that for some unaccountable reason the even-year population has maintained its dominance since the earliest available records. Tremendous numbers of pink salmon are recorded at Karluk in 1880 by Bean (1891) and in 1890 by Moser (1899); both of which are even years. The

tches since 1908 in area 8 at the mouth of the arluk (available through 1935) and the weir unts are shown in table 9.

ABLE 9.—*Catches of pink salmon at mouth of Karluk River (Area 8) and weir counts of pinks*

[In thousands]

ven years	Catches	Weir counts	Odd years	Catches	Weir counts
8	233		1909		
0	105		1911	9	
2	293		1913	12	
4	1,287		1915	13	
6	2,319		1917	1	
8	336		1919	6	
0	635		1921		
2	894		1923	10	
4	2,483	[1] 4,000	1925	6	
6	86	15	1927	3	
8	18	5	1929		12
0	1	116	1931	140	43
2	1,388	1,440	1933	32	108
4	1,048	1,002	1935	7	6
6	?	526	1937	?	6
8		1,715	1939		32
0		957	1941		133
2		[2] 107	1943		[2] 0.2
4		193	1945		[3] 16
6		[3] 83	1947		0.05
8		41	1949		0.05
0		87	1951		0.04
2		37	1953		0.1

[1] Estimated.
[2] Weir moved from river mouth upstream to Portage near head of Larsen r.
[3] Weir moved to outlet of Karluk Lake.

The most striking feature shown by these data the ability of the even-year pink runs to recover er overpopulation (as in 1924) has decimated em. The odd-year runs, on the other hand, ve never been able to achieve dominance. om table 9 we have constructed figure 15, which shows for the odd years from 1929 to 1943 (before the counting weir was moved to the lake outlet) the number of pink salmon returning per spawner plotted against the number of pinks spawning in the preceding (even) year. There is some suggestion that the return per spawner in an odd year is inversely related to the number of pinks spawning in the preceding even year. The explanation is not contained in the data; we can only surmise concerning the relationship.

If the relationship is due to predator activity it is necessary to postulate a predator having both a high reproductive potential and a short life history. One might also speculate on the possibility of contamination of the spawning beds by some etiological agent that would destroy most of the eggs or fry of the year following a big year spawning.

Neave (1952) in attempting to explain this odd- and even-year disparity says:

> Attention was especially directed to the probable effect of predators during the migration of salmon fry to the sea, in inflicting relatively heavier losses on smaller populations. When a population exceeds or falls below certain limits of size it is likely to be subject to influences which tend to maintain the direction of change or at least to oppose a return to the former level.

His explanation is too simple in that it cannot explain the quick rise of the even-year cycle to abundance after falling below the odd year in numbers.

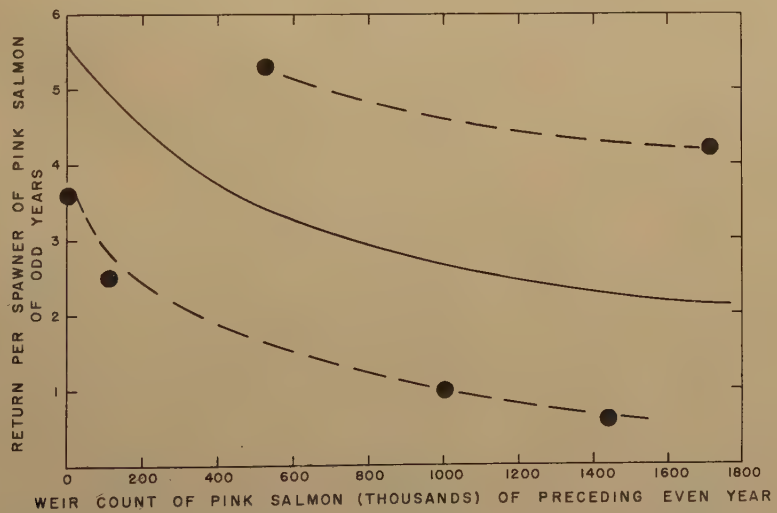


FIGURE 15.—Apparent relation between the return per spawner for pink salmon of odd-numbered years and the weir count of pink salmon of each preceding even-numbered year.

However, it is beyond the scope of this paper to inquire into the many factors that may operate to maintain the dominance of one pink salmon population (in this case the population spawning on the even-numbered years) over another. The chief purpose of this digression has been to show that this phenomenon has existed at Karluk as far back as our records go. Thus we may, with considerable confidence, assume that the even-year pink runs exceeded those of the odd years during those periods in which we lack data on pink-salmon abundance.

Regardless of the cause of the even-year dominance in the pink salmon it is possible to decide whether it has a significant effect on the survival of sockeye. In table 10 are shown the numbers of sockeye (corrected for the four physical factors already discussed) that returned from the spawning escapements of the 60 years from 1889 to 1948, inclusive.

An analysis of variance is as follows:

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Total	59	764, 331. 184		
Odd and even	1	16, 968. 017	16, 968. 017	5. 724*
Cycle years	4	128, 433. 6	32, 108. 4	10. 831**
10-year periods	5	473, 664. 884	94, 732. 977	
Within cycle years (error)	49	145, 264. 683	2, 964. 585	

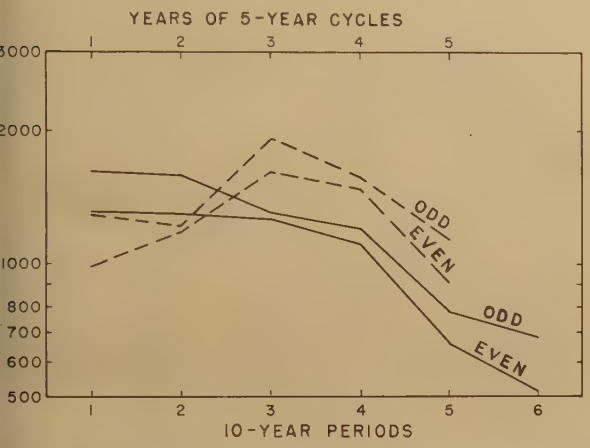
TABLE 10.—*Returns corrected for physical factors*
[In ten thousands]

First year of spawning in 5-year cycle	Year of cycle										5-year cycle	10-year period	
	1		2		3		4		5			Odd	Even
	Odd	Even	Odd	Even	Odd	Even	Odd	Even	Odd	Even			
1889	326			207	318			252	148		1, 251		
1894		128	408			559	418			167	1, 680		
Sums	454		615		877		670		315		2, 931	1, 618	1, 313
1899	232			337	539			398	251		1, 757		
1904		232	206			167	354			160	1, 119		
Sums	464		543		706		752		411		2, 876	1, 582	1, 294
1909	178			230	343			346	161		1, 258		
1914		172	245			375	374			136	1, 302		
Sums	350		475		718		720		297		2, 560	1, 301	1, 259
1919	238			258	404			209	262		1, 371		
1924		175	100			284	195			187	941		
Sums	413		358		688		404		449		2, 312	1, 199	1, 113
1929	98			59	234			197	170		758		
1934		168	97			139	176			92	672		
Sums	266		156		373		373		262		1, 430	775	665
1939	217			84	95			76	140		612		
1944		108	162			81	67			164	582		
Sums	325		246		176		143		304		1, 194	681	513
Odd and even sums	1, 289	983	1, 218	1, 175	1, 933	1, 605	1, 584	1, 478	1, 132	906			
Sum of cycles	2, 272		2, 393		3, 538		3, 062		2, 038		13, 303		
Sums of 10-year periods											13, 303	7, 156	6, 147
10-year averages											221. 717	238. 53	204. 9

$\frac{221.717}{238.53} = .929514$

$\frac{221.717}{204.9} = 1.082074$

This shows that the returns in the odd years
e significantly higher than in the even years.
rthermore, this difference does not occur in
phazard fashion. The odd-year returns are
gher than the even-year returns in each of the
10-year periods and also within each of the 5
cle years. In figure 16 the logarithms of the
btotals for odd- and even-year returns are shown
th for 10-year periods and for cycle years (from



GURE 16.—Logarithms of the subtotals for odd- and even-year pink salmon returns for both 5-year cycles (broken line) and for 10-year periods.

table 10). This shows no particular trend but rather that the difference is quite consistent.

Because the logarithmic differences between odd and even years are both consistent and fairly constant, the returns shown in table 10 have been corrected to equalize the difference by multiplying the even years by the factor 1.082074, or 221.717/204.9 and the odd years by the factor 0.929514 or 221.717/238.53. The corrected returns are given in table 11.

The chief manner in which the even-year pink salmon runs may affect the even-year sockeye runs is through direct competition for spawning space. Since the pinks spawn later than most of the sockeye they can destroy many of the sockeye redds in years in which large numbers of pinks reach the lake. How often does this occur? From the records of field parties visiting the lake in various years this would appear to happen only on even years when pinks are especially numerous. Thus in 1924 when the escapement of pink salmon to the river was estimated at 4 million, it is estimated by Gilbert and Rich (1927) that one-fourth to one-third of this number entered the lake. However, in 1932 when the weir count showed 1,440,000 pinks, J. T. Barnaby (field

TABLE 11.—*Returns corrected for physical factors and for odd- and even-numbered years*

[In thousands]

Year of spawning	Returns	Returns per spawner	Log return per spawner (+ 1.0)	Residuals of log return vs. spawners (× 10)	Year of spawning	Returns	Returns per spawner	Log return per spawner (+ 1.0)	Residuals of log return vs. spawners (× 10)
	2,921	5.40	1.732	.72	1918	1,475	2.45	1.389	−1.89
	3,496	2.47	1.393	.85	1919	2,212	3.72	1.571	.11
	3,029	1.84	1.265	.37	1920	2,795	3.79	1.579	.45
	2,238	1.61	1.207	−1.08	1921	3,751	2.50	1.398	1.19
	2,961	1.88	1.274	.24	1922	2,264	5.66	1.753	1.05
	2,721	2.36	1.373	−.21	1923	2,435	3.50	1.544	−.04
	1,380	1.17	1.068	−3.14	1924	1,898	1.79	1.253	−1.72
	1,382	.97	.987	−3.16	1925	934	.58	.763	−4.74
	3,795	5.24	1.719	1.80	1926	3,071	1.21	1.083	1.53
	6,044	5.42	1.734	3.06	1927	1,815	2.08	1.318	−1.70
	3,883	4.41	1.644	1.58	1928	2,025	1.85	1.267	−1.47
	1,811	3.48	1.542	−.68	1929	913	1.01	1.004	−1.51
	2,152	4.81	1.682	.50	1930	635	.58	.763	−3.26
	3,650	3.27	1.515	1.10	1931	2,175	2.49	1.396	2.36
	5,013	2.57	1.410	2.85	1932	2,132	2.89	1.461	2.57
	4,303	2.94	1.468	1.78	1933	1,584	1.64	1.215	.85
	2,333	4.07	1.610	.22	1934	1,820	1.26	1.100	.42
	2,513	2.85	1.455	−.30	1935	903	1.03	1.013	−1.47
	1,916	1.99	1.299	−1.60	1936	1,503	1.09	1.037	.42
	1,810	.98	.991	−1.73	1937	1,634	1.29	1.111	.98
	3,286	2.08	1.318	.66	1938	999	.81	.908	1.34
	1,733	2.00	1.301	−1.74	1939	2,021	2.86	1.456	2.40
	1,657	3.33	1.522	−.96	1940	909	1.11	1.045	−1.35
	2,488	3.09	1.490	−.24	1941	884	.95	.978	−1.64
	3,192	3.44	1.537	.66	1942	823	1.31	1.117	−1.26
	3,748	5.59	1.747	1.91	1943	1,301	1.41	1.149	.14
	1,497	3.21	1.507	−1.22	1944	1,173	1.53	1.185	.06
	1,861	6.40	1.806	1.20	1945	1,501	2.28	1.358	1.26
	2,280	5.11	1.708	.77	1946	875	1.98	1.297	−.08
	4,058	3.38	1.529	1.51	1947	622	1.28	1.107	−1.83
	3,480	2.75	1.439	.83	1948	1,770	2.35	1.371	1.70

notes) observed "not over 100 pinks" on the spawning streams entering Karluk Lake.

This evidence from examination of the spawning streams is difficult to evaluate for two reasons. First, because the field parties attempted to visit the lake during the height of the sockeye spawning, and thus may sometimes have missed the pink salmon that arrived later. Secondly, after the weir was moved from downriver to the lake outlet in 1945 some pinks have passed through in every season, varying from less than a hundred to 16,000 in odd years and from 37,000 to 87,000 in even years.

It is our guess that a larger and more constant fraction of the pink salmon population enters the lake each year than was formerly supposed. This helps to explain the consistency with which the odd year sockeye returns exceed those of the even years.

It is probable that this reflection of the pink salmon cycle in the returns from sockeyes spawning the same season also may indicate that a larger proportion of the sockeyes spawn in the main river below Karluk Lake than available records would indicate (see appendix L).

TYPE OF REPRODUCTION CURVE

In order to study the changes in the sockeye population it is desirable to understand the manner in which the size of the population changes. Many of the theoretical considerations are rather fully discussed by Ricker (1954). Under conditions in which there are definite spatial limitations he suggests a domed reproduction curve. If we let x equal number of spawners, and y equal the number of adult salmon returning, his formula is:

$$y=xe^{1-x} \text{ or } \log y=\log x+(1-x).$$

His method of fitting by trial and error is too cumbersome, however. We have used a linear least square fit. The formula is:

$$\log y/x=a-bx \text{ or } \log y=(a-bx)+\log x$$

which is equivalent to his formula as it can be expressed as

$$y=xe^{a-bx}.$$

The regression of the $\log_{10}$ return per spawner (from table 11) on number of spawners,

$$\log y/x=a-bx$$

is shown in figures 17 and 18. The data were broken into two periods 1887–1928 and 1929–1948

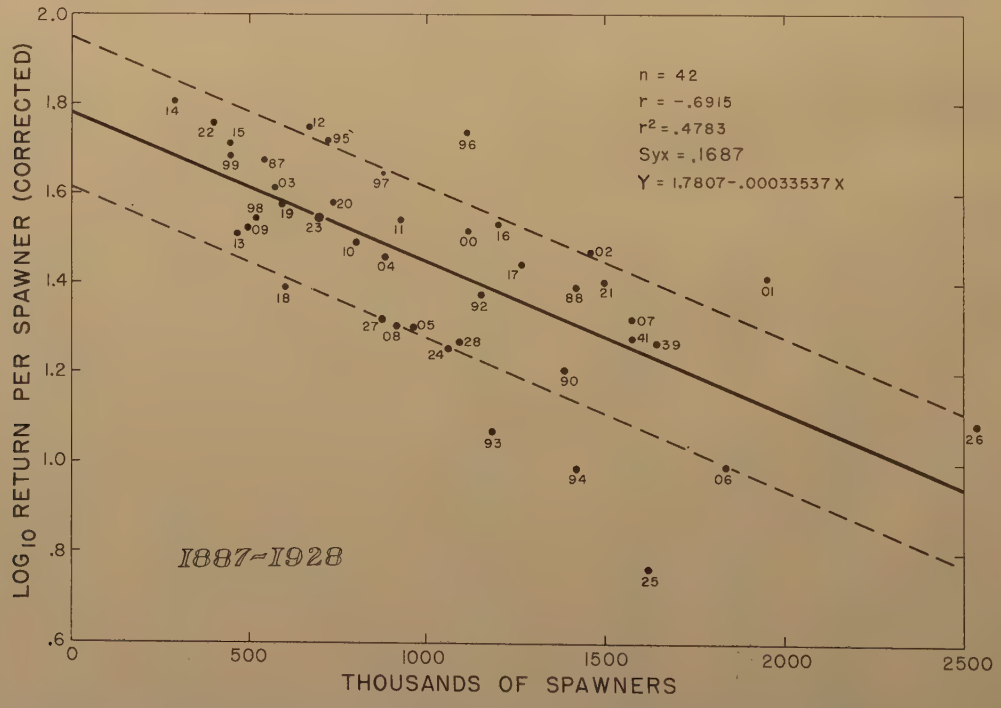


FIGURE 17.—Regression of log return per spawner (corrected for physical environment and for odd and even years) on number of spawners for 1887 to 1928 period.

s there is a definite break after 1928. It will be oted that the two slope coefficients, b, are very imilar, 0.0003354 and 0.0003347, also, the stand-rd errors of estimate 0.1687 and 0.1696.

This means that the two reproduction curves re practically identical, except for the level of eproduction. This is shown in figures 19 and 20. n figure 19 is also shown the curve resulting from the linear fit of the return per spawner on log number of spawners:

$$y/x = a - b \log x \text{ or } y = (a - b \log x)x$$

which is equivalent to log $y = x\epsilon^{a-b \log x}$. This curve gives a slightly better fit to the data, r is $-.752$ whereas for the other curve r is $-.692$. However, the second curve eventually cuts the

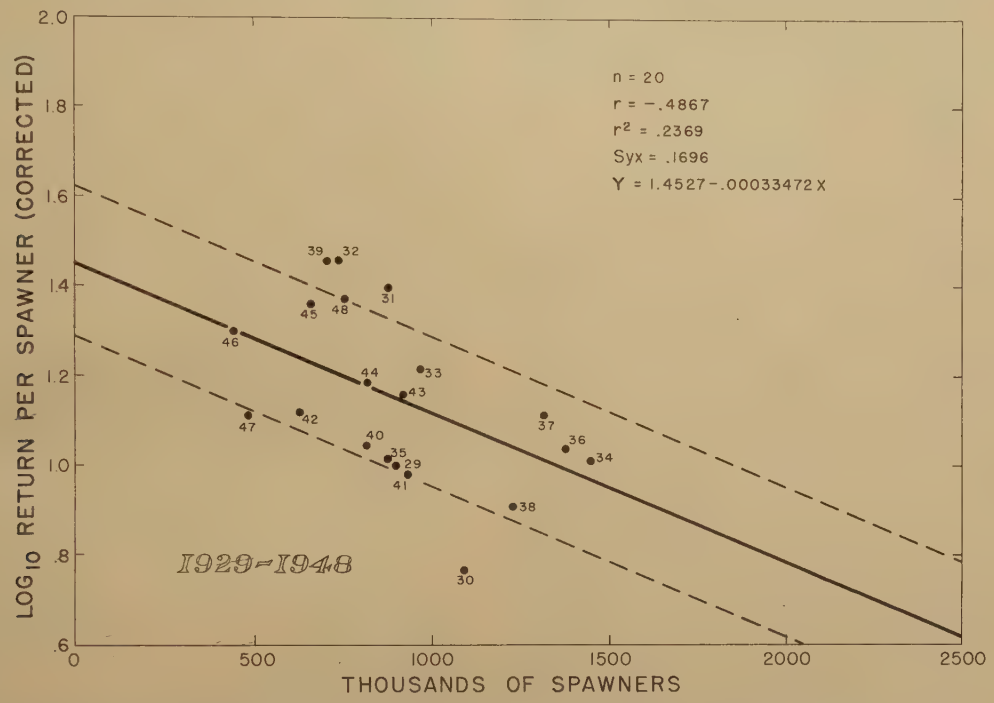


FIGURE 18.—Regression of log return per spawner (corrected for physical environment and for odd and even years) on number of spawners for 1929–48 period.

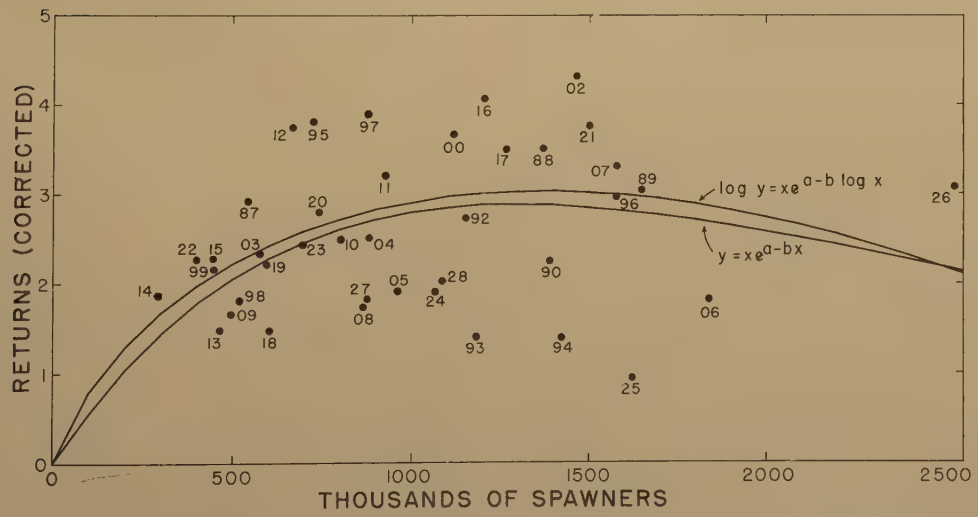


FIGURE 19.—Returns (corrected) on number of spawners for the 1887 to 1928 period.

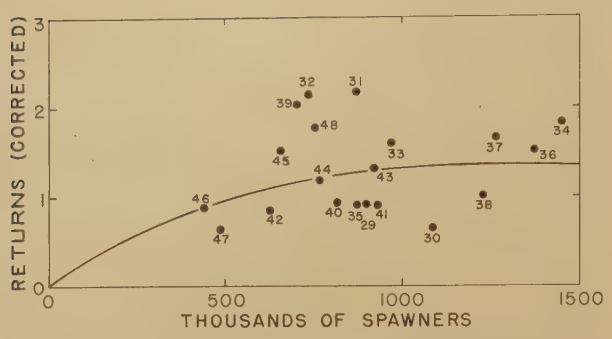


FIGURE 20.—Returns (corrected) on number of spawners for the 1929 to 1948 period.

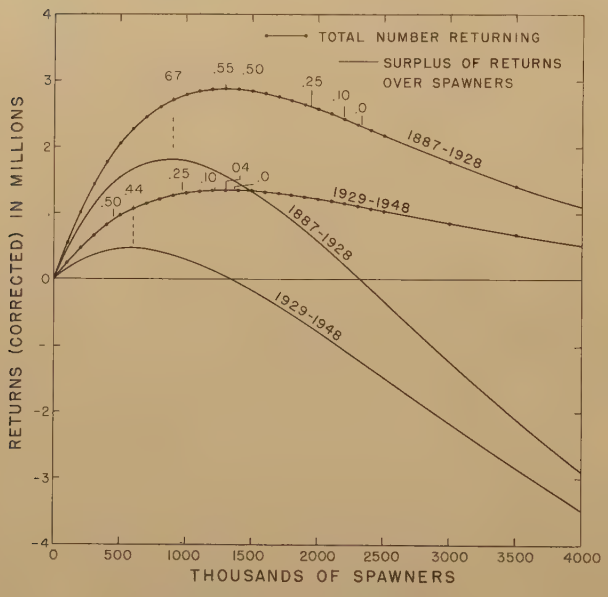


FIGURE 21.—Reproduction curves (corrected for physical factors and for odd and even years) showing the returns for various numbers of spawners, and also the surplus of returns over number of spawners.

base line, which the first curve approaches asymptotically. From this standpoint the first curve is probably more realistic.

MEANING OF REPRODUCTION CURVES

The reproduction curves for the period 1887–1928 and for the more recent 20-year period from 1929–48 are shown in figure 21 together with the resulting surpluses of returns over number of spawners. It will be noted that for the earlier period the returns were approximately double those of the later period for an equivalent number of spawners. However, this caused a tremendous difference in the available surplus.

During the early period the highest surplus, 1,811,000 occurred with 900,000 spawners, whereas during the later period the highest surplus, 472,000 occurred with 600,000 spawners. The average number of spawners was 1,037,000 in the earlier years and 894,000 in the later.

On the curves in figure 21 are indicated the equilibrium points for various rates of removal by the fishery of the returning adults. For the earlier years the largest returns occurred at a removal rate of .55 and the largest available surplus (on a continuing basis) occurred at a rate of .67. By way of contrast the same points for the later years occurred at rates of .04 and .44.

Owing to the varying effect of the various environmental factors the abundance would, of course, fluctuate about these points. However, in general, the average abundance in the earlier period, in the absence of any fishery, would have been about 2,320,000. As the fishery developed the number of spawners would be decreased and the population would ascend the right limb of the reproduction curve, resulting in larger runs. That this bears some relation to reality is shown by the stability of the runs during the first three cycles of the fully developed fishery as follows:

Years	*Returns (table 6)*
1887–91	15, 986, 000
1892–96	14, 051, 000
1897–01	16, 339, 000

The paramount question is what caused the long-term decline in the runs. Certainly the decline was not due to lack of a sufficient number of spawners. However, as will be shown later, the spawners have not been drawn equally from all parts of the run. This has meant that although 50 percent of the number in each migration have been permitted to spawn, the reproductive potential of the 50 percent allowed to spawn was less than 50 percent of the reproductive potential in the original migration. Thus, although there has not been overfishing in the usually accepted sense of taking too many fish, it appears likely that there may have been overfishing by taking too high a proportion of the fish with the highest reproductive potential.

The long-term decline cannot be ascribed to the effects of those changes in temperature and rainfall or in pink salmon abundance, which we have discounted through the removal of most of their effects.

There is one peculiarity of the sockeye population at Karluk that has not been adequately explained, namely, the 5-year "cycles" in the size of the run. For many years these cycles were both persistent and consistent but in the late 1920's the "dominant" years of the past (the 1891 and 1892 cycles) lost their dominance; in fact, the 5-year cycles became rather obscure. This can be seen in figure 22 which shows the ratio of each year's return to the moving 5-year average.

In 10 successive cycle years the 1891 and 1892 cycles each fell below the 5-year trend once dur-

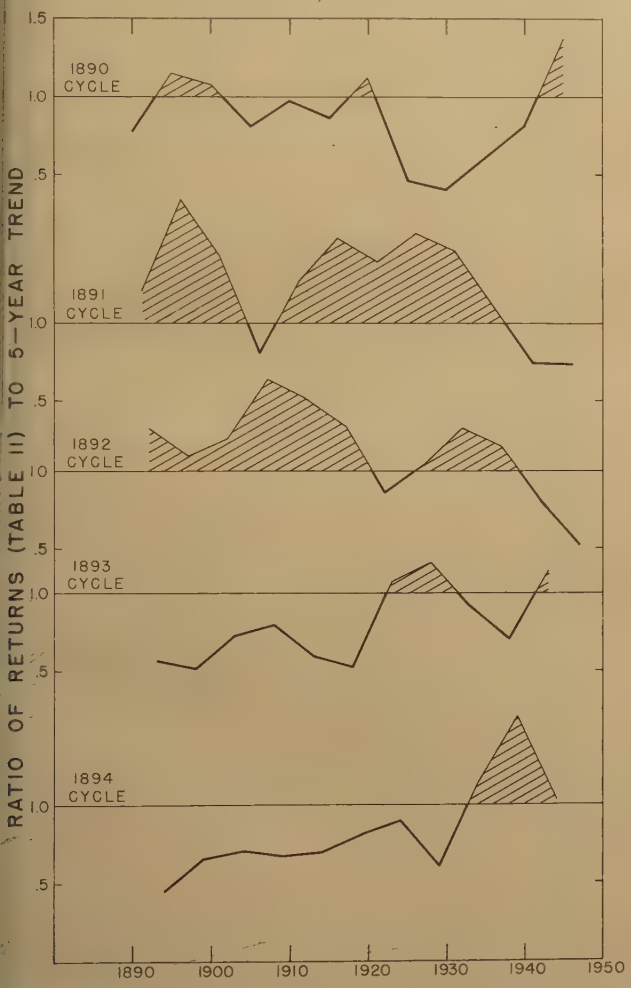


FIGURE 22.—Ratio of each year's returns to that of a 5-year moving average of returns by 5-year cycles commencing in 1890, 1891, 1892, 1893, and 1894.

ing the early years of the fishery. The lowest cycle for abundance was that of 1894 which fell well below the trend for 8 successive cycle years.

These cycles have not gone unnoticed in the past. Gilbert and Rich (1927) state:

> Since the Karluk salmon are predominately five-year fish, we anticipate a correlation between the run of any year and that of the fifth year preceding, the fifth year following, etc. With the exception of one of the six cycles, it is apparent from the graph that the Karluk runs consist of two good years followed by three poor years—the good years are those ending in the figures 1, 2, 6, and 7, and the poor years end in the figures 3, 4, 5, 8, 9, and 0.
>
> No one can examine such a series of data without being impressed by the conspicuous correlation between the size of the catch in the corresponding years of the several cycles. There is a remarkably uniform tendency in each cycle, as shown on the graph, for the catch of the second year to be smaller than that of the first, for that of the third to be smaller than that of the second, for the catch of the fourth year to be about the same as that of the third, and for that of the fifth year to be greater than that of the fourth. If it can safely be assumed that spawning escapements are in the main roughly proportional to the catch, it becomes apparent that they are the predominating factor in determining the size of the runs.

Barnaby (1944) states:

> It can be concluded from the fact that a statistically significant correlation of over 0.6 exists between the catches at 5-year intervals and that no statistically significant correlation exists between the catches at 4-year or 6-year intervals that the runs of Karluk red salmon from 1895 to 1921, inclusive, were composed largely of 5-year fish.

As a result of the force of logic, that 5-year cycles should be expected from fish that mature chiefly at 5 years of age (and die after spawning), this view that the cycles are the result of age composition has been rather generally accepted, and until recently has gone largely unchallenged. It will be especially noted that this cyclic effect, if dependent on number of spawners, must postulate equal returns per spawner for all sizes of spawning escapements. That this is not true is clear from figure 21. The return per spawner continually declines as the number of spawners increases. The same phenomenon is apparent in the sockeye runs to the Fraser River (Rounsefell 1949, fig. 4).

The view that age alone could not account for cycle dominance is discussed at length by Ricker (1950). He states concerning the Fraser:

> The old big cycle had persisted through many decades of the historical period and for an undetermined period previously. Right up to the time it was accidentally destroyed it showed no signs of diminishing its domination of the river. This fact at once suggests that the big cycle somehow was acting unfavorably upon the off cycles, and actually prevented them from becoming numerous.

The equilibrium points for several rates of exploitation are shown in figure 21. Under any constant rate of fishing, regardless of the number of spawners one commences with, the number returning in successive generations will move toward these equilibrium points. It becomes obvious then, that the continued existence of dominant cycle years must depend upon some density-dependent reaction between the various years, whereby the big years tend to keep down the small years, and vice versa.

Gilbert and Rich (1927) state:

> With the present requirement of a minimum escapement of 1,000,000 fish, which has been in force since 1925, it is hoped that the level of productivity may once again be raised, but it will not be until the season of 1930 that the catch will be affected by the regulation.

The attempt to raise the size of the returns, especially in the off years, by requiring a minimum escapement (this was in addition to the requirement of a 50-percent escapement) did not bring forth the hoped-for results. It did soon destroy the dominance of the former "big" years, but without a concomitant increase in the runs.

We have attempted to explore this relation between years as it affects the returns from each year by examining the data for density-dependent relations between brood years.

The residuals of $\log_{10}$ returns per spawner (from table 11) against number of spawners are shown in table 11, column 5. These residuals are plotted in figure 23 against $\log_{10}$ ratio of the corrected returns for each year (from table 11) divided by the average observed return for the second and third preceding year. The observed returns (by freshwater age) of sockeye that would have been in the lake in their third and fourth year of life (from table A5 of Appendix C) are used as a measure of the density of 3- and 4-year-old young sockeye in the lake during the season that the fry of the year in question are emerging from

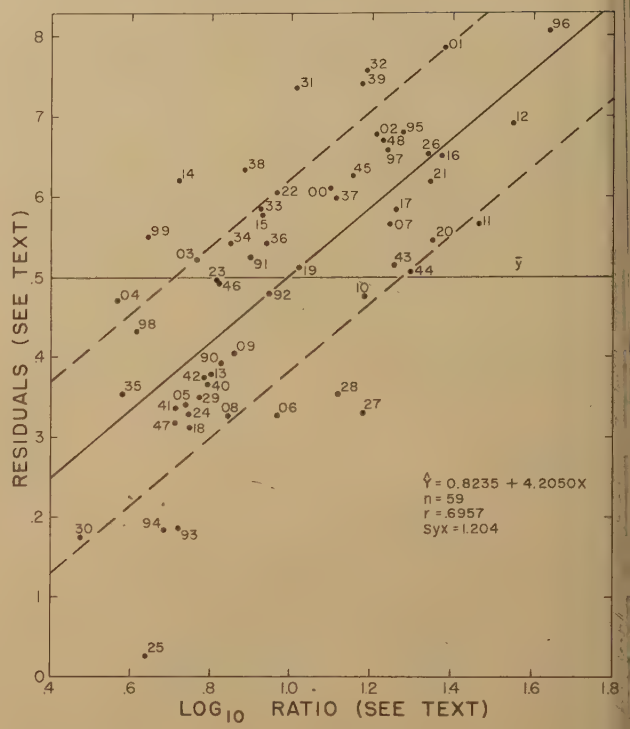


FIGURE 23.—Residuals (corrected, see text) of log return per spawner on number of spawners plotted against the logarithm of the ratio of each brood's returns to that of the average returns for the second and third preceding years.

the gravels of the tributary streams and of the lake itself. The relationship is close; r is .70.

This indicates that for any particular number of spawners the expected return per spawner is increased or decreased, according to the relative density of 3- and 4-year-old sockeye in the lake.

Although lacking the data to prove the actual existence of this phenomenon, Ricker (1950) hints that such a relation is indicated by the persistent dominance of particular cycles in the Fraser River sockeye. He states:

> Although the great bulk of sockeye food is plankton, there is a good possibility that these older sockeye, particularly after they have lived for two growing seasons, can consume young sockeye fry of later cycles. This has not yet been observed, but residual sockeye of 2 years of age have been found to eat young fish of other species, so there is little reason to doubt that they can consume sockeye fry.

Residual sockeye are known to occur in Karluk Lake. Ricker (1940) states,

> . . . J. T. Barnaby has informed the writer that, in the course of his investigations of Karluk Lake, Kodiak Island, Alaska, he has obtained three specimens of residual sock-

e. It should be noticed, however, that before gill-nets re used in 1932, their existence in Cultus Lake was not spected; and since very few sockeye lakes have been plored in this manner, it may even be that they occur turally wherever there is an anadromous stock.

The young sockeye migrating from Karluk Lake erage very much larger, and older, than those Cultus Lake (fig. A4), so there is an even eater probability that the older groups of young nsume large quantities of the fry. The existce of such a relationship may help to explain w the dominant cycle year can occasionally fall ry low (the returns from the year class of 1906, ble 6), yet rapidly regain its ascendancy, since e young from such a poor dominant cycle year 1906 are not exposed to the same high density older sockeye as are the low cycle years. milarly, even when environmental conditions low a fair return from one of the low cycle years is pushed down again in the succeeding cycle nen the young are again exposed to high density older young.

It will be noted that this relationship can explain e apparent 5-year periodicity in the runs. The use of the periodicity is not the 5-year age of aturity (based on a positive regression), but the ke density of young sockeye (based on a negative regression). This negative regression being for conditions 2½ years previous (effect of 3 and 4 year olds on 1 year olds) would, of course, cause an apparent positive 5-year cycle.

The residuals of the $\log_{10}$ return per spawner against log ratio of returns to the average observed return for 2 and 3 years before were corrected for this negative regression. The corrected log return per spawner is in table 12, column 2. The regressions of the corrected log return per spawner on number of spawners appear in figures 24 and 25, and the regression of total corrected returns on number of spawners appears in figure 26.

The effect of removal of the variability caused by lake density of the older young sockeye can be seen by comparing figures 21 and 26. The steeper slope of the right limb of the earlier return curve of figure 26 indicates that during the earlier years the large returns from large numbers of spawners were aided by the presence of cycles whereby the fry of the "dominant" cycle years encountered a lower density of older young in the lake.

With this effect of lake density removed the earlier years would have produced the highest returns with less than 1,100,000 spawners instead

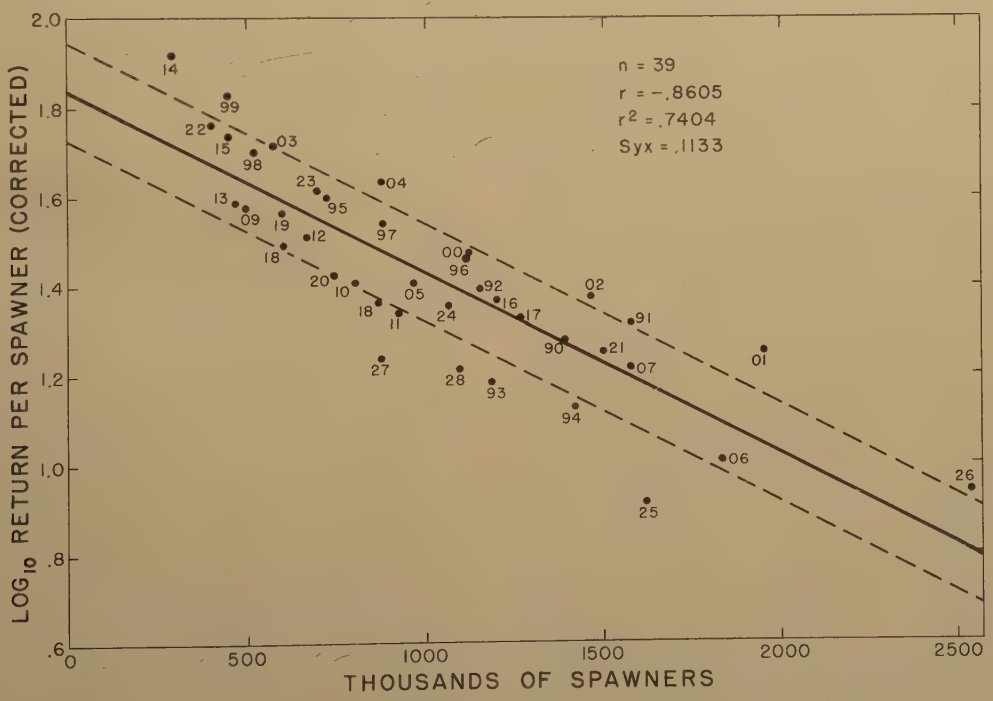


FIGURE 24.—Regression of log return per spawner (corrected for six factors, see text) on number of spawners for the 1887 to 1928 period.

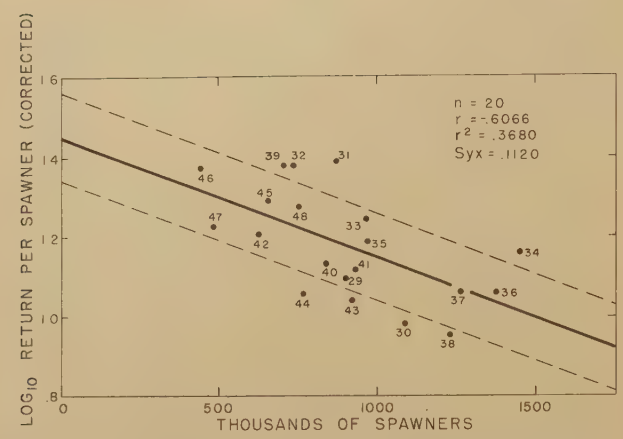


FIGURE 25.—Regression of log return per spawner (corrected for six factors, see text) on number of spawners for the 1929–48 period.

of with 1,300,000 and the greatest surplus with 750,000 spawners instead of with 900,000. Thus figure 26 shows that when the lake density factor is removed the earlier and later years approach much closer in the optimum number of spawners required to produce the maximum surplus. In figure 21 the points were at 900,000 and 600,000 spawners, whereas with the lake density factor removed the points are at 750,000 and 650,000 spawners.

TABLE 12.—*Returns corrected for climate, for odd- and even-numbered years, and for density of young in the lake, 1890–1948*

Year of spawning	Corrected log return per spawner (+1.0)	Corrected return per spawner	Total corrected return	Year of spawning	Corrected log return per spawner (+1.0)	Corrected return per spawner	Total corrected return
1890	1.276	1.852	2,572	1920	1.426	2.667	1,968
1891	1.312	2.051	3,239	1921	1.248	1.770	2,655
1892	1.391	2.460	2,834	1922	1.762	5.781	2,312
1893	1.183	1.524	1,804	1923	1.617	4.140	2,877
1894	1.125	1.334	1,896	1924	1.356	2.270	2,413
1895	1.599	3.972	2,876	1925	.911	.815	1,321
1896	1.461	2.891	3,223	1926	.936	.863	2,187
1897	1.539	3.460	3,045	1927	1.237	1.726	1,505
1898	1.701	5.024	2,612	1928	1.212	1.629	1,782
1899	1.828	6.730	3,008	1929	1.096	1.236	1,114
1900	1.470	2.951	3,296	1930	.982	.959	1,042
1901	1.246	1.762	3,443	1931	1.387	2.436	2,127
1902	1.375	2.371	3,466	1932	1.377	2.382	1,758
1903	1.706	5.082	2,912	1933	1.242	1.746	1,690
1904	1.633	4.295	3,792	1934	1.158	1.438	2,085
1905	1.406	2.547	2,453	1935	1.186	1.535	1,345
1906	1.001	1.002	1,842	1936	1.057	1.140	1,568
1907	1.211	1.626	2,566	1937	1.060	1.148	1,452
1908	1.362	2.301	1,993	1938	.952	.895	1,101
1909	1.576	3.767	1,876	1939	1.378	2.388	1,686
1910	1.408	2.559	2,057	1940	1.128	1.342	1,095
1911	1.337	2.173	2,017	1941	1.094	1.242	1,158
1912	1.511	3.243	2,173	1942	1.203	1.596	1,004
1913	1.587	3.864	1,804	1943	1.036	1.086	1,000
1914	1.917	8.260	2,404	1944	1.056	1.138	875
1915	1.733	5.408	2,412	1945	1.289	1.945	1,282
1916	1.367	2.328	2,798	1946	1.368	2.333	1,031
1917	1.325	2.114	2,674	1947	1.224	1.675	812
1918	1.491	3.097	1,867	1948	1.271	1.866	1,407
1919	1.561	3.639	2,165				

REASONS FOR LONG-TERM DECLINE IN ABUNDANCE

The foregoing analyses indicate that when most of the environmental sources of variability are removed there remains a high residual relationship between the number of spawners and the expected returns. The return per spawner decreases logarithmically as the number of spawners increases, resulting in a domed reproduction curve.

The 5-year periodicity in the runs appears to have been caused by the effect of the lake density of older young on the survival of the young of subsequent years. The decreased periodicity in recent years through the decline of the former "dominant" years may have been brought about largely by the increased proportion of the run, which through regulation has been permitted to spawn in the low years of abundance. The more even rate of competition between older young and the fry of each brood resulting from this loss of periodicity in the runs may have contributed to the general decline (fig. 32).

The possible role of predators in bringing about the decline in the Karluk returns has always been largely dismissed because it was thought that overfishing alone was the cause. In more recent years, as large escapements failed to bring large returns, there has been a school of thought that suggests a declining productivity of the waters.

It is apparent that the decrease in the size of returns in recent years cannot be assigned to overfishing of the spawning stock in the usually accepted meaning of the term. The spawning stock has been kept high through strict control of the catch, so that the decline is not caused by an insufficient number of spawners. The decline becomes apparent in a lowered return per spawner.

Aside from fishing, there are two chief sources of mortality, and it is to changes in these sources of mortality that we must look for an explanation of the changes in rate of survival as shown by the lowered return per spawner in recent years. These sources can be listed under two headings: physical and biological.

Changes in mortality caused directly or indirectly by changes in the physical environment we have discounted as far as the data warrant. Although the physical factors exhibit variations that often trend in one direction for several years,

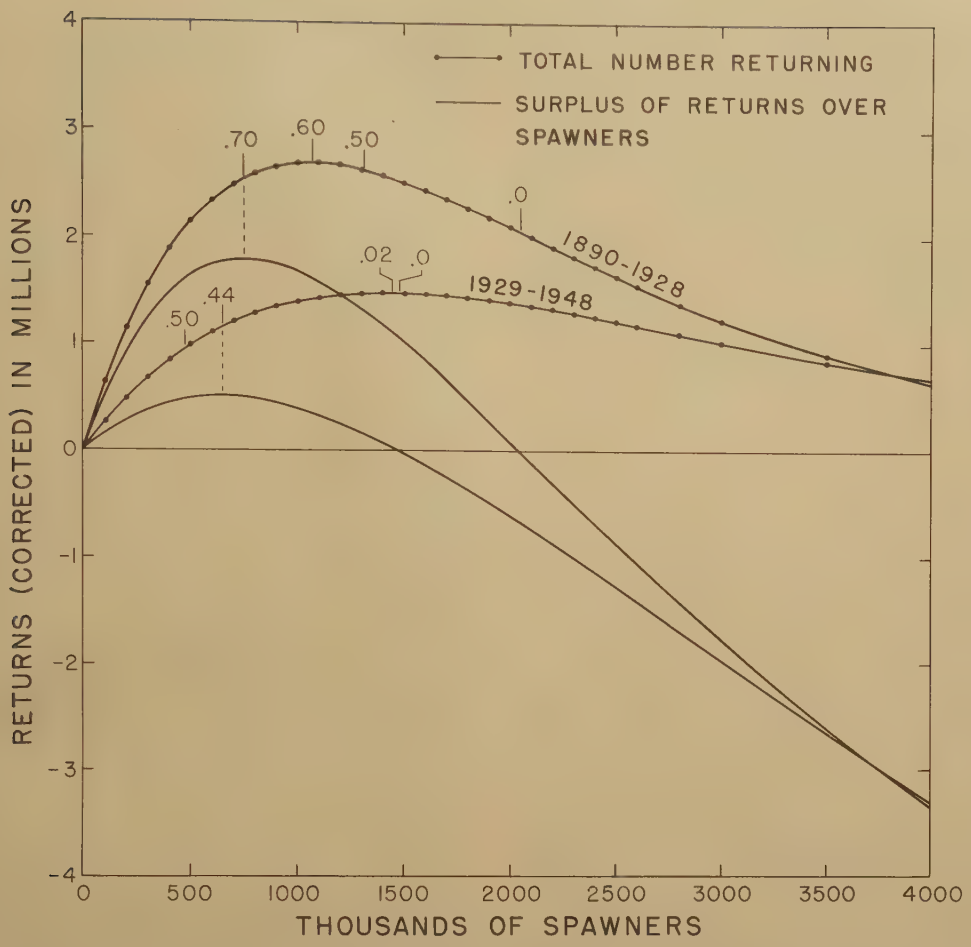


FIGURE 26.—Reproduction curves (corrected for physical factors, odd and even years, and lake density of older young) showing for early and later periods the returns for various numbers of spawners, and also the surplus of returns over number of spawners. The figures along the curves are the equilibrium points for several fishing rates.

ere are no long-term trends in the available servations to indicate that the physical environ-ent can be charged with the long-term decline. The second source of mortality is to be found the biological environment, which can affect ortality in several ways.

ect of spatial competition on mortality

This may be primarily the cause of the domed ape of the reproduction curve, caused by low-d survival to the fry stage as increased numbers spawners spread out over the less suitable avels or destroy each other's redds on over-owded beds. Spatial competition may also be e important factor in the difference in the rate survival between fry of the odd- and even-mbered years. However, the odd- and even-ar difference has been present throughout the period of years considered, so that the recent decline in abundance cannot be ascribed to it.

It is of interest to note that with the larger spawning escapements there is not only a lowered survival per spawner, but the total survival is less. There are two possible explanations for this seeming anomaly. One is that when a spawning bed is badly overcrowded the fish have difficulty in spawning effectively. A pair cannot always hold an area undisturbed but are pushed about by the dense mass of fish and it is probable that many eggs are not properly buried. Likewise, in order to find unoccupied territory the salmon utilize unsuitable beds. This is indicated for instance by field notes of Henry O'Malley and Dr. Charles H. Gilbert in their 1919 trip to Karluk Lake (Gilbert and Rich 1927, p. 13), which state,

About half way on west side is a creek (Grassy Point creek) about 6 feet wide and now 6 inches deep, thickly beset with dead and living fish. Temperature 46°. In the lowest 1,000 feet (paced) we counted 1,400 dead salmon, and estimated that side branches contained as many more (4,800 in all), and that there are fully as many live salmon as dead ones. It is safe to say, counting those now preparing to enter the mouth, that there are 10,000 fish spawning in the lower 1,000 feet of the stream. Apparently about 1 mile of stream with spawning in progress, and probably 50,000 fish in all.

Gulls were thick at mouth of creek and some were encountered higher up. They were feeding on drifting eggs, which could be seen in every eddy. Creek bottom of coarse cobbles and gravel, very hard, apparently not dug up. Seems impossible eggs could be buried, and loss must be enormous.

A second cause of lower total survival from the larger escapements may be the destruction of spawn by the spawning activities of the late-comers. Thus Gilbert and Rich (1927, p. 20–21) quote from the field notes taken by Fred R. Lucas in 1924 as follows:

O'Malley River.—Red salmon were spawning in this stream in larger numbers than ever noticed before by the writer. Believe it would average a pair to each square yard, except in the so-called "pothole," where they had spawned earlier. Two visits in August in previous years disclosed comparatively few fish in this stream. Apparently the red spawning here is at its height in September. Thousands of humpbacks had spawned here and some red eggs had been dug out. The reds were now digging out the humpback eggs. Behind every rock and in every eddy piles of humpback eggs lay. Within 22 steps the writer counted 12 piles that would average 5 gallons to a pile; and behind a small island about 6 feet in diameter there were more than a 50-gallon barrel full of humpback eggs. These eggs were all dead; had been dug out and drifted around before passing the tender stage. A small percentage of red eggs was among them . . .

Canyon Creek.—This is the best red stream on the lake this year. Some dead humpbacks were at the lower end, but live and dead reds were thick all the way to the falls. Some of the early red eggs are being dug out by present spawners.

Thumb River.—More reds spawning here than in previous years. . . . Great numbers of humpbacks have spawned here and the reds are now busily working over the same ground. Humpback eggs, with some red eggs, were piled in heaps in eddies and shallows on the right-hand side. Apparently the humpbacks had dug up the early red nests, and what eggs were past the tender stage were still alive but drifting around.

It was thought by Gilbert and Rich (1927) that despite these unavoidable losses the total egg deposition was larger in years of large runs and they so state:

Undoubtedly the late comers dig up many of the nests of those that came earlier, and destroy a regrettably large number of eggs; but they replace those they destroy with fresh lots of their own eggs, and many of the earlier eggs must escape destruction. Even in years of very heavy runs, when waste of eggs is excessive, the net result is probably a more complete seeding of all available gravel than occurs during runs of more moderate dimensions.

Gilbert and Rich are probably correct in assuming that larger numbers of spawners usually leave more eggs in the spawning gravels than smaller numbers. There are no present data, however, to indicate the relative numbers of fry emerging. It is entirely possible that the disturbance of the earlier spawned eggs that are not dug out (some still in the tender age) combined with the additional growth and spread of fungus helped by the large numbers of widely distributed crushed eggs may greatly lower the fry production from an over-spawned bed. Another possible explanation may be the lack of sufficient oxygen in the gravel to satisfy the requirements of too large an egg deposit. Wickett (1954) has demonstrated for chum salmon eggs in Nile Creek that some portions of a spawning bed may lack sufficient oxygen and that this may be aggravated by siltation.

Effect of competition for food on mortality

This can be treated under two headings, i. e. interspecific and intraspecific competition. It would be extremely difficult to believe that the decline could be ascribed to intraspecific competition for food. For such to be the case one would have to postulate a tremendous decrease in the production of food organisms, because the recent runs of less than one-half the earlier runs would scarcely be so drastically affected unless the food supply was also very drastically reduced. As a matter of fact the difference between the food requirements for the early and late periods should be measured by the size of the runs of adjacent years since the young of two broods are both abundant in the lake at the same time. The highest and the lowest totals for runs of any 2 adjacent years in each of the six 10-year periods for the observed returns (table 6) are:

10-year period	Total returns in thousands for 2 adjacent years		Lowest/highest
	Highest	Lowest	
			Percent
1889–98	9,760	2,762	0.2
1899–1908	9,760	3,250	.3
1909–18	7,049	2,105	.3
1919–28	7,434	2,416	.3
1929–38	5,116	2,511	.4
1939–48	2,689	1,182	.4

The 2 highest adjacent years out of the last 10 re only 28 percent of the highest of the 1889–98 eriod. This would be in the order of a fourfold eduction in food production before it could even art to have an effect on the present populations.

The relative importance of the parts played by umber of migrants as against size of migrants in etermining the number of returning adults has ot been clearly settled. This is often because vailable data are not adequate, either in kind or uantity to properly test the hypothesis.

Foerster (1954) says of Cultus Lake sockeye ata for an 18-year period that:

> Analysis of these data indicates a negative correlation etween size of migration (in number of smolts) and ercentage return of adults which is found (by multiple rrelation treatment) to be related principally to the size eight in grams) of the smolts.

From the data published by Foerster (1954, p. 42) the following statistics have been calculated which x_1 equals log of average smolt weight, x_2 quals log of number of smolts and y equals log f adults returning:

$_2$=−.7268** r_{y_1}=−.2601

r_{y_2}=.6758** R=.7549**

nce r_{12} shows a very high negative correlation etween average weight and number of smolts, is important to consider the partial correlations hich are:

$r_{13.2}$=.4564 $P>.05$ and $r_{23.1}$=.7340 $P<.01$

$r^2_{13.2}$=.2083 and $r^2_{23.1}$=.5387

R^2_4=.5126

These partial correlations indicate that the fluence on the number of returning adults of dividual smolt weight is only about 21 percent ($^2_{13.2}$=.2083), whereas the influence of number of nolts is about 54 percent ($r^2_{23.1}$=.5387). Furtherore, the influence of smolt weight may not be gnificant as P is greater than .05.

A further analysis was made in which x equals g of the weight of the biomass of smolts of each ood and y equals log of the adults returning: equals .753**, and r^2=.57 which is a little larger an $r^2_{y_2}$ of .46 when y is estimated from number smolts alone. (See figure 27.)

It is evident that at Cultus Lake the variality in returns is related chiefly to changes in umbers of smolts, and only in small degree to anges in average weight.

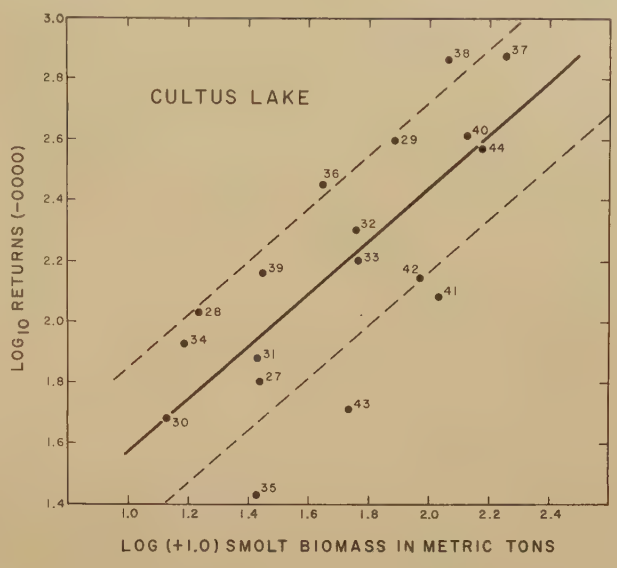


FIGURE 27.—Regression of log return on log biomass of smolts for Cultus Lake, British Columbia (data from Foerster 1954).

At Karluk over a 14-year period from 1923–37 (except 1933, see appendix J) the length of 3-year smolts showed a positive correlation coefficient of .60 with the number migrating, which is the reverse of conditions at Cultus Lake where size and number showed a high negative correlation. This can probably be explained by the fact that at Cultus Lake the young sockeye population (fig. 29) is larger in relation to its food supply than at Karluk.

Further evidence that competition for food is not the important factor at Karluk is shown by analysis of the smolt production (see tables A–9 through A–12 in Appendix F). Table A–9 and figure A–4 show that the Cultus Lake smolts, although very small as they leave the lake in their second year, are heavier for their length than those from Karluk. The Babine Lake smolts of the Skeena River appear to be intermediate. These characteristics are a function of form and are of no significance in themselves.

In tables A–10 and A–11 the total biomass of the smolt migrations is shown for Karluk and Cultus Lakes for periods of 15 and 18 years, respectively. For Karluk Lake the linear correlation between biomass and number of smolts is 0.968 (fig. 28). It is obvious that the runs during the 15-year period considered were not sufficiently large for the smolts to compete for the available food supply. Considering the reduced size of the

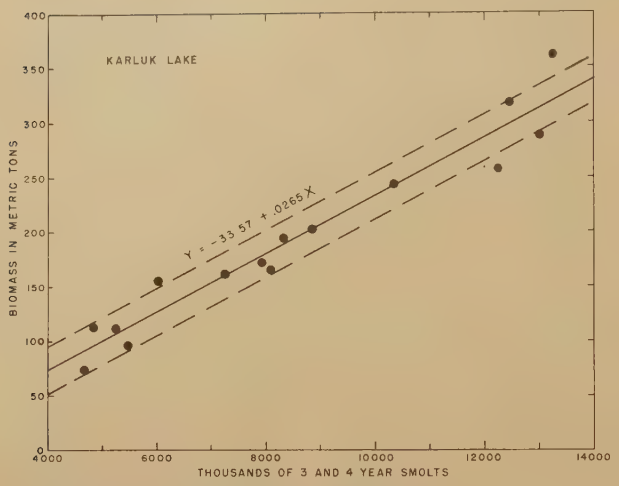


FIGURE 28.—Regression of biomass of migrating smolts on number of smolts for Karluk Lake, 1926–40.

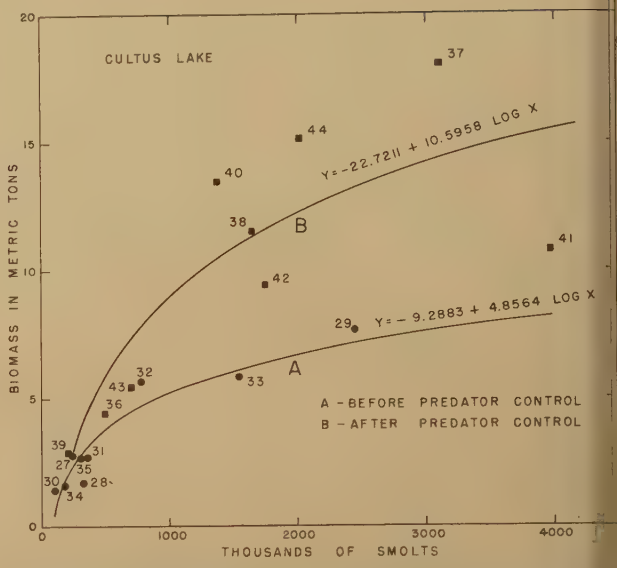


FIGURE 29.—Regressions of biomass of migrating smolts on log number of smolts for Cultus Lake, 1927–44.

populations of recent years compared with past years, this is a logical sequence if the food supply is unimpaired.

Furthermore, the slope of the regression line shows that the smolts from larger populations were actually larger individually. This suggests that although there may be no food competition between the young of a year class at Karluk, the relative survival of each year class may be dependent on the annual food density so that the survival is highest when growth is fastest.

The reverse is apparently true for Cultus Lake. In figure 29 are shown the curves for biomass versus the logarithm of the number of smolts. The correlation coefficients for biomass versus log number of smolts are 0.95 for the 9 years before control of predators (and food competitors, e. g., squawfish (*Ptychocheilus oregonensis*)), and 0.83 for the 9 years following the institution of controls. Both correlation coefficients have a probability of less than 0.01.

It would appear that the food supply of Cultus Lake is insufficient to enable the biomass of smolts to increase in proportion to their numbers. The closeness of the semilogarithmic fit suggests immediately that the increasing competition between smolts as their numbers increase sets an asymptotic level on the biomass. This level was apparently doubled by control of the numbers of other fishes.

As is shown by Ricker and Foerster (1948) the higher the survival rate of the young the smaller will be the loss of production through mortality of young which have already consumed a portion of the available food. Therefore, the raising of the asymptotic level approached by the weight of the biomass of migrating smolts can occur within limits without any increase in available food merely through raising survival by curbing loss due to predation.

The weight of the smolt biomass migrating from Karluk Lake is truly amazing. The average comes to 41.4 pounds per acre (table A–12). The total standing crop of all fishes from 51 North American lakes (Rounsefell 1946) is less than 40 pounds per acre in lakes over 100 acres. The annual sport and commercial take of fish from the highly productive Wilson reservoir in Tennessee with 15,500 acres is only 32.0 pounds per acre. It must be remembered that the biomass of migrating smolts does not include the great mass of younger parr remaining in the lake. The lake is also inhabited by large populations of both alpine and Dolly Varden charrs, young of coho and king salmon, young steelheads, and quantities of sticklebacks.

Most of the available limnological data for Karluk and Cultus Lakes are not strictly comparable. Perhaps the best comparison of their potential productivity is shown by the differences in water transparency. From Juday et al. (1932)

nd Ricker (1937b) the following Secchi disc eadings in meters are extracted:

Lake	July	September	October
humb	3.6	2.5	
Malley	4.8	3.9	
arluk	7.2	6.8	
ultus		16.2	16.0

Although the Cultus Lake readings were very ant Ricker says in confirmation,

> In the course of taking plankton samples from 1932 ward the instruments could be seen as they descended, own to 13–15 metres, throughout most of the year.

It would be difficult to believe that the difference n smolt biomass production between Karluk and ultus Lakes could be entirely dependent upon ne difference in plankton production. The effect f another related factor, namely, temperature, lso merits consideration.

The best data available on the effect of water emperature on growth of young sockeye are ontained in an excellent report by Donaldson nd Foster (1941). They held groups of sockeye ngerlings for 6 months in six tanks with indi- idually controlled water temperatures and re- orded by fortnightly intervals the grams of food onsumed and grams of change in the total weight r each lot of fish. Using these data we have lotted figure 30 showing the efficiency of growth increase or decrease in weight of fish/weight of ood fed) against water temperature. The points n the empirical curve are grouped averages.

Figure 30 shows that like all cold-blooded ertebrates the sockeye is restricted in the range f temperatures suitable for growth. As expected rowth is very slow below 40° F., increasing apidly with increase in temperature until a lateau of favorable growth conditions is reached xtending from about 45° to 68° F. The optimum ange of temperatures is about 48° to 56° F., after vhich growth declines gradually with increasing emperature up to about 67.5°. At this point he growth curve falls steeply, and above 70° F. he sockeye lose weight.

Available data concerning the surface water emperatures of Karluk and Cultus Lakes (Ricker 937b; Juday et al., 1932; and Barnaby 1944) are hown in figure 31. Except for 1935 and 1936 the Karluk observations are scant. However, for the years with observations only 1926 and 1936 both warm years) show any surface temperatures

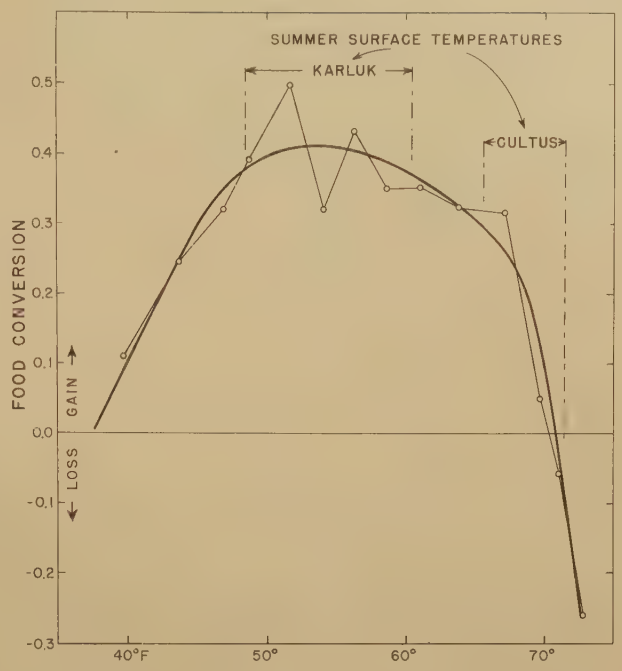


FIGURE 30.—Growth of young sockeye in 2-week periods, as shown by food conversion, at different water temperatures (data from Donaldson and Foster, 1941). For superimposed summer surface lake temperatures see figure 31.

above 14° C. At Cultus Lake for the 3 years of observations none fell below 19° C. after June 20 until September 14, a period of 85 days or 12 weeks.

It is clear that whereas the surface waters of Karluk Lake are seldom if ever too warm for efficient growth of young sockeye, the surface waters of Cultus Lake become too warm for an extended period in midsummer. Foerster (1937) shows that the annual migration of smolts from Cultus Lake terminates as the surface temperature rises. Over an 8-year period 80 percent of the smolt migration on the average had passed out of the lake by the time the surface water reached 10.6° C.; the maximum was reached in 1935 when 80 percent were out at a temperature of 12.5° C. When the temperature reached 13° C., the daily migrations decreased greatly. On the average, the migrations ceased entirely at 17.5° C. (range from 14.4° in 1930 to 20.1° in 1933).

Foerster comments,

> It is suggested, therefore, that the cessation of migration is definitely related to the creation in the epilimnial waters of the lake of a temperature blanket through which yearling sockeye, presumably late in responding to the

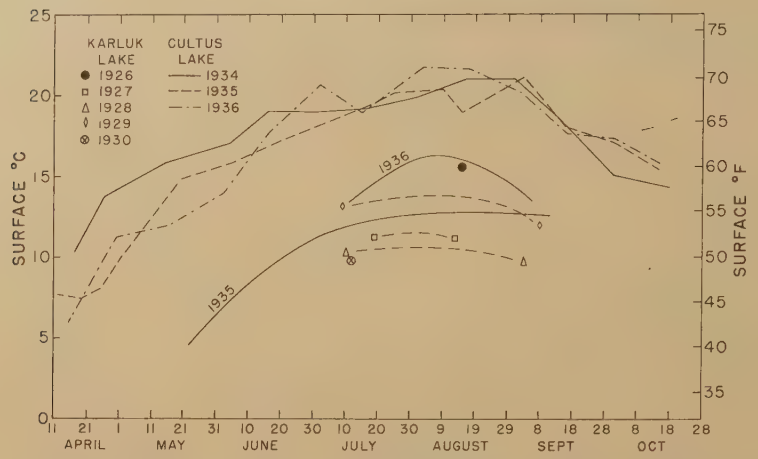


FIGURE 31.—Surface water temperatures during the warm season at Cultus Lake, 1934 to 1936 (upper curves), and at Karluk Lake in various years from 1927 to 1936 (lower shorter curves). Individual readings for 1935 and 1936 at Karluk omitted.

migration stimulus, are unable to pass. As a result they return to the deeper waters of the lake, there to remain until the migratory influence is again felt the following spring.

At Karluk Lake the smolt migration is much later than at Cultus Lake; the height of the migration at Karluk occurs during the first two weeks in June, whereas the Cultus Lake migration reaches its height in April. Furthermore, at Karluk the migration continues into July. There is other evidence that the young utilize the surface waters during the warmer parts of the year.

Gilbert and Rich (1927) quote from the field notes of E. M. Ball for September 13, 1917, while at Karluk Lake,

> From sundown, until darkness prevented further observation, the lake was alive with feeding fingerlings.

Even though the young sockeye are pelagic in the lake they are occasionally caught with beach seines, i. e., J. T. Barnaby collected them with a seine on August 8 and September 18, 1927.

Bare Lake, a small lake in the Red River drainage only 12 air miles from Karluk, is too shallow to have a thermocline, yet it has a regular run of sockeye.

It would appear that Cultus Lake is in reality marginal for sockeye because of the high summer temperatures which force the salmon to live in the narrow stratum of water adjacent to and beneath the thermocline. In Karluk Lake, on the contrary, the young can feed at the surface throughout the summer. This is the most logical explanation of the vast superiority of Karluk Lake for growth and for total production per area sockeye smolts.

Effect on mortality of intraspecific competition wh could take the form of cannibalism

As shown by the analysis of the effect of l density of young sockeye on the survival of fut broods, this is probably an important cause fluctuations in survival. The importance of t factor can best be grasped by comparing curves for the later with those from the ear years, before the "dominant" cycle years h been destroyed (fig. 32). Obviously the effect intraspecific competition was to raise the survi from the larger spawning stocks of the domin years and to lower the survival from the low y broods, the young of which would feel the f pressure of competition in the lake from numerous young of the dominant years.

During this early period the above describ effect gave the dominant cycle years an advant in survival that kept them dominant despite variations in survival from other causes. equal number of spawners in an off year yielde lower return than in a dominant year, because young had to face a larger number of young fr the previous dominant broods. The net res was a tendency for the years with domin broods to remain large and the years of low bro to remain small.

When the take of the fishery was regulated permit a larger proportion of spawners in the l years this delicately-balanced natural cycle w

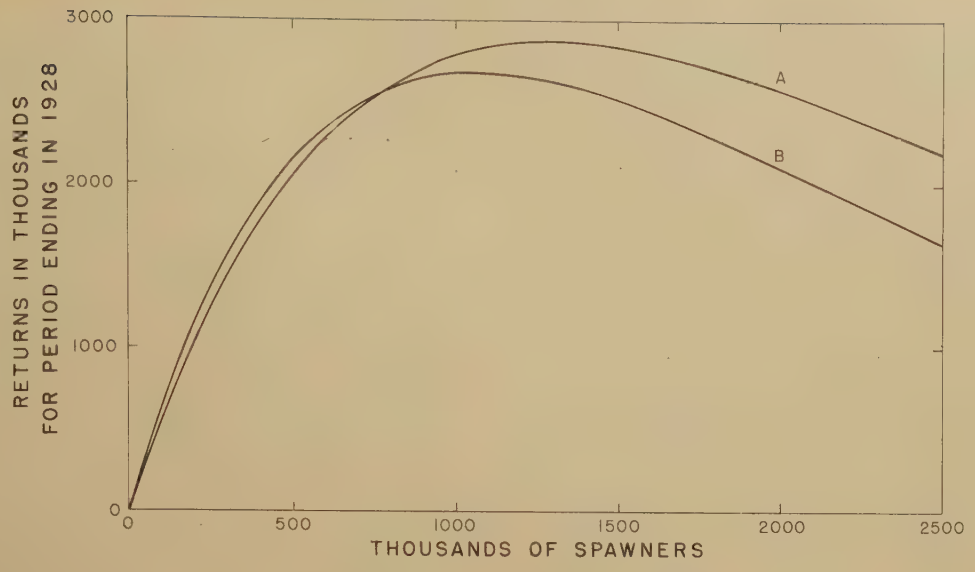


FIGURE 32.—Reproduction curves derived from return per spawner on number of spawners for the period of years ending in 1928 showing curves corrected (*B*) and uncorrected (*A*) for lake density of the older young at time of fry emergence.

stroyed. This tended to equalize the intra-ecific competition between years.

fect of predation on mortality

The sockeye in fresh water has numerous preda-rs: bears, mergansers, gulls, young of the coho d king salmon (*Oncorhynchus kisutch* and *O. awytscha*), the steelhead rainbow trout (*Salmo irdneri*), the fresh-water sculpin (*Cottus aleuti-s*), the Dolly Varden trout or charr (*Salvelinus lma*) and its close cousin, the alpine charr or d lake charr (*Salvelinus alpinus*).

Although the data are admittedly meager we n form some notion of the probable abundance predators and the amount of depredation. In ing so it would be best to try to make some fferentiation between types of predators. The st type, (1) are those that may fluctuate in undance independently of the abundance of ckeye. They may be referred to as nondensity-pendent. The second type, (2) are those that pend sufficiently on sockeye for food so that eir abundance is controlled, at least to a signifi-nt extent, by the abundance of sockeye. They e referred to as density-dependent predators.

Predators of the first type would be more apt take a rather fixed number of sockeye, irrespec-ve of sockeye abundance. Their net effect ould be to render it difficult for sockeye in years low abundance to recuperate until they pass a threshold of abundance sufficient to offset the amount taken by the predator. As a matter of fact, when the escapement is sufficiently large for the expected return to fall along the right limb of the reproduction curve (fig. 32), the loss of some adult spawners could actually increase the expected return.

Predators of this first type include land mammals. Shuman (1950) dismisses predation by the smaller mammals as insignificant, but stresses the high predation by the Kodiak bear, which he believes increased in numbers at Karluk in the 1940's owing to the absence of hunters, natural increment, and migration from areas occupied by military installations.

From actual weir counts of bear-killed salmon in Moraine Creek, a tributary of Karluk Lake, as well as observations on bear-killed salmon and on incidence of bears on other streams he estimated a minimum bear kill of unspawned salmon of 94,000 in 1947, which would be 19.4 percent of the escapement of 485,000. A large bear population could account for an appreciable portion of the difference in the returns per salmon between early and late years, since predation by bears could be important when runs are small.

Predators of the first type also include birds. Assessment of damage is difficult for many species of birds because of the variety of foods taken.

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The bald eagle will attack adult salmon in the streams, but there is no reason to believe that eagles are of any but minor importance as predators.

The American merganser, according to White (1937), rears its broods on the streams where it consumes large quantities of salmon and trout, although it will eat any fish available. Its appetite is enormous; he found that a young bird ate an average of more than a third of its own weight each day.

In contrast to White's findings on Cape Breton Island, Munro and Clemens (1937) found in British Columbia, that salmon were not so important an item, and that they ate more fresh-water sculpins. However, mergansers were collected throughout the year. Salmon were an important item in certain localities, especially during the downstream fry migration in the spring. Although mergansers eat salmon eggs, they believed that the eggs eaten were largely loose eggs not buried in the gravel, which would constitute a loss in any event.

Young sockeye salmon could be subject to merganser predation at two periods. The first would be after emergence from the gravel and before completing the descent to the lake; the second would be during the smolt migration from the lake to the sea. As mergansers also take fresh-water sculpins, young trout, and stream-dwelling young coho and king salmon, it would be a difficult task to judge the balance between beneficial and harmful effects without extensive data.

Birds were stressed as destructive by Bean (1891):

> Chief among the destroyers of the young fish are terns, gulls, ducks, and loons, which are very common in that region. I shot some terns and gulls near the south end of Karluk Lake and upon holding them up by the legs small salmon dropped out of their mouths. Towards the end of August the shallow parts of Karluk River were visited by hundreds of gulls, chiefly young of *Larus glaucescens* and *L. brachyrhynchus*, which were feeding upon young salmon.

This is at variance with the findings of Munro (1928) in British Columbia. Here the glaucous-winged gull was feeding on salmon carcasses and loose salmon eggs. In August the main Karluk River would be unlikely to contain many sockeye fry, but there might be fry of the coho and king salmon. When Bean visited Karluk in the summer of 1889 there should have been numerous pink salmon fry from the even-year spawning of 1888, but towards the end of August seems late for pink salmon fry to remain in fresh water, and there would seem to be some question concerning the chief food of the concentration of gulls observed.

For the fish predators it would be advantageous to know whether or not their density is dependent on the density of sockeye. There is some information bearing on this subject for the coho salmon, *Oncorhynchus kisutch*, at Cultus Lake. Foerster and Ricker (1953) give the mean length of lake-residing coho salmon in their third year together with the number of sockeye migrants leaving the lake the same spring and the mean December-to-March air temperature before the migration. Their data cover 6 years and they found no statistically significant correlations. However, if one employs the logarithm of the number of sockeye migrants the correlation with coho length is .71 (r is .75 for P of .05). The multiple correlation coefficient of coho size on temperature and on the logarithm of number of sockeye migrants is .80 (R is .81 for P of .05), indicating that the growth of young coho is increased by an increase in abundance of young sockeye.

The existence of a marked relationship between coho growth and number of young sockeye in the lake is a strong indication that the survival of coho from young to adult is influenced strongly by young sockeye abundance. This follows because it has been shown by many investigators that the larger coho smolts have a higher rate of survival from time of seaward migration until their return. At Karluk this relationship holds between smolt size and survival for the sockeye so that it is reasonable to assume that at Karluk it also holds for the coho.

This view that the coho depend largely on young sockeye at Cultus Lake is stated by Ricker (1941):

> Coho are perhaps the only species which would suffer severely from a scarcity of sockeye, for their only considerable alternative food is insects, which during much of the year are not available.

A count of coho salmon was not made during every year at Karluk, and in many years the weir was removed before the last of the coho had ascended. By averaging the weekly count by the number of years with available data it was possible to arrive at an estimate of the average coho escapement (table 13). During 10 years of the 1926–37 period the average escapement through

he weir near the river mouth was nearly 21,000. n 1945 the weir was placed at the outlet of arluk Lake. In the 9 years from 1945–53 the verage escapement into the lake was about 8,800 hoes, sufficient to maintain a large number of oung coho predators.

ABLE 13.—*Escapement of coho salmon by weeks when weir was at river mouth and at lake outlet*

Week ending	1926–28 and 1931–37		1945–53		Average counts	
	Count	Number of years	Count	Number of years	Early period at lower weir	Later period at lake outlet
ug. 23			9	4		2
ug. 30	3,345	4	237	6	836	40
pt. 6	3,531	7	722	7	504	103
pt. 13	15,406	9	1,973	8	1,712	247
pt. 20	42,776	10	8,219	8	4,278	1,027
pt. 27	79,371	10	9,815	8	7,937	1,227
ct. 4	26,309	10	18,260	9	2,631	2,029
ct. 11	22,422	10	15,561	5	2,242	3,112
ct. 18	1,575	2	1,929	2	788	964
ct. 25			69	1		69
Sum					20,928	8,820

The most numerous of the fish predators are he two charrs. DeLacy and Morton (1943) made study of these charrs at Karluk. They state:

Perhaps the most conspicuous feature in the life history f the dolly varden is its habit of migrating regularly to nd from salt water. At Karluk the seaward movement ccurs in the latter part of May and in early June. Al- hough the majority of the population participates in the igration, it is known that some dolly vardens remain ehind, because adult representatives of the species are resent in the Karluk system during late June and early uly, at a period when no charrs are moving either up or own the river. The return migration from salt water to esh water takes place from mid-July until September fter an average residence in the ocean of approximately 0 days, as determined from tagging experiments.

Concerning the red lake or alpine charr they tate:

Until late June, insects are the most common food eaten y these charrs. As soon as the red salmon begin to spawn n the tributaries of the lake in late June or early July, chools of lake charr may be found congregated about the outh of each stream. At this time of the year they eat ot only the salmon eggs that drift downstream into the ake, but also other food material dislodged in the streams y the spawning salmon. Later in the season as the dis- ntegrating carcasses of the dead, spawned-out salmon ccumulate in the lake, fragments of this flesh become the ost common item in the diet of the lake charr. Fish aught in shallow portions of the lake feed heavily on ticklebacks during certain seasons. Cottids, salmon ingerlings, and young charr are found occasionally in heir stomachs. During September, insect material again esumes its earlier position as an important source of food.

The great abundance of these charrs is attested by the numbers that have been caught and destroyed during the down-stream migration of the Dolly Varden. This ran as high as 82,000 in 1937 and over 50,000 in 1938 and again in 1939. Considering that these represent only a portion of the Dolly Varden population, it is plain that the two charr populations require a great quantity of food.

That these charrs can be destructive to young fry migrating down-stream is shown by Pritchard (1936) whose data we have summarized in table 14. It should be noted that the coho described above as being density dependent on sockeye abundance took fewer fry than the Dolly Varden.

Barnaby (1938, p. 33) says,

At Karluk Lake it was noted that charrs take a very heavy toll of red salmon fry in the spring at the time the young fish are entering the lake from the spawning streams.

The destructiveness of the Dolly Varden charr is attested also by Ricker (1933) who states concerning their predation at Cultus Lake,

Individually these are more destructive to sockeye thar are any other fish in the lake. The specimens taken in the nets ranged from eleven to twenty-seven inches in length, and all fed largely upon young salmon. The greatest numbers were found in May and in mid-July, when stomachs contained an average of 17 sockeye each, and individual fish had as many as 90.

The predation was not confined to the large Dolly Varden, he adds that,

A number of Dolly Varden, 5–6 inches long, were taken at the counting fence in the outlet of the lake during the spring migration of yearling sockeye. Even these small fish were able to eat the migrant sockeye, as well as many small coho fingerlings.

If we make the wholly reasonable assumption that these charr populations increase in the wake of a large spawning of sockeye and decrease after a small spawning we can readily perceive how they might be an important factor in causing long-term changes in the rate of survival.

While discussing predation mention should be made of another species abundant in Karluk Lake, the 3-spined stickleback, *Gasterosteus aculeatus*. Evermann and Goldsborough (1907, p. 273, listed as *G. cataphractus*) mention specimens collected from a large school in Karluk River near the Lake in 1903 by Cloudsley Rutter that ranged from 2 to 4 inches. There seems to be little

TABLE 14.—*Food of predator fish in McClinton Creek, British Columbia, during springs of 1931 and 1933* (from Pritchard 1936)

Species of predator	Number of specimens	Number of salmon fry in stomachs	Number of stomachs empty	Number of stomachs containing insects	Salmon fry per specimen	Common name of predator
Cottus sp.	165	187	98	1	1.1	Freshwater sculpin.
Salvelinus malma	76	616	6	1	8.1	Dolly Varden charr.
Salmo clarki	11	12	6	0	1.1	Cut-throat trout.
Oncorhynchus kisutch [1] and *S. clarki*	1,523	3,917	188	17	2.6	Mixed.[1]
Oncorhynchus kisutch	385	1,072	76	0	2.8	Coho salmon.
All species	2,160	5,804	374	19	2.7	

[1] Estimated by Pritchard to be over ninety percent *O. kisutch*.

evidence that they are actual predators. Kincaid (1919) says,

> The damage done by the Stickleback is out of proportion to his size as he is able to kill the fry of larger fish, notably the salmon, for which reason the Stickleback is known locally as the salmon killer.

Bigelow and Schroeder (1953, p. 309) say of the same species,

> It is a proverbially pugnacious fish, using its spines with good effect as weapons of offense and defense, even on fishes much larger than itself. It feeds indiscriminately on the smaller invertebrates, on small fish fry, and on fish eggs, to which it is exceedingly destructive in fresh water.

Concrete evidence of destruction of salmon fry by sticklebacks appears to be lacking. White (1930) carried out experiments in 1927 and 1928 in which he placed 1,000 trout fry each (*Salvelinus fontinalis*) in screened sections of a stream. In one section he added 200 adult 3-spined sticklebacks, in another he placed 25 larger trout, and in both years he tried one section with both 200 sticklebacks and 25 larger trout. Losses in the last experiment were 85 percent in both years. Losses with trout alone were 78.6 percent and with sticklebacks alone 54.4 percent. Unfortunately, no controls were run to determine survival in the absence of either trout or sticklebacks. However, the difference between the 85 percent and the 78.6 percent with and without sticklebacks is too small to even consider its significance.

Salmon fry are much larger than the fry of the brook trout, so that there would seem to be even less chance of any destruction.

During the earlier years when the fluctuations in the runs were of greater magnitude the predator populations would have had a large range in size, whereas in later years, when the range of fluctuations was much less, the predator populations likewise would fluctuate less. Under such conditions it would be difficult for salmon of the dominant years to become re-established. The effort to obtain a large number of spawners in every year would assure the predators a constant food supply, and the fry of all brood years would be subject to heavy predation.

There is the possibility that during the period when the runs were cyclic in character the frequent occurrence of years with low numbers of spawners aided in keeping the predator populations under control. Table 15 gives the frequency of the numbers of spawners in the early and late periods. During the early period, 10 years, or nearly 1 year out of 4 had less than 600,000 spawners, whereas in the later period only 3 years, or 1 year in 8, had so few spawners. The large number of spawners in many of the early years may have aided also in controlling predators, since their large increase in numbers following the big years would render them more susceptible of damage in the low years.

TABLE 15.—*Frequency of number of sockeye salmon spawners (in thousands)*

Number of spawners	1887–1928	1929–53
200–300	1	
301–400	1	
401–500	4	2
501–600	4	1
601–700	3	4
701–800	2	6
801–900	5	3
901–1,000	2	4
1,001–1,100	2	1
1,101–1,200	4	
1,201–1,300	2	2
1,301–1,400	1	1
1,401–1,500	4	1
1,501–1,600	2	
1,601–1,700	2	
1,701–1,800		
1,801–1,900	9	
1,901–2,000	1	
above 2,000	1	
Total	42	25

The difference between the early and recent periods in number of spawners is perhaps better illustrated by the differences between the minimal and maximal numbers. Since a 5-year cycle is being discussed and as the two series of years are unequal in number, perhaps the best measure is afforded by comparing the 20th and 80th percentiles of the frequencies in table 15 as follows:

Percentiles	Frequency class	
	Early years	Recent years
	501–600	601–700
	901–1,000	701–800
	1,801–1,900	1,001–1,100
80–20	1,300	400
(80–20)/50	1.37	0.53

This comparison shows that the amplitude of the oscillations between high and low numbers of spawners was over twice as great in the earlier years in the more recent period.

Effect on mortality of age of smolts at migration

The Karluk smolts average about 3 to 4 times heavier than those from Cultus Lake. While all but a small minority of Cultus Lake smolts migrate in the spring of their second year, the second year migration at Karluk is very small. The majority migrate in their third year, a fair number leave in their fourth year, and small numbers leave in their second and fifth years (table 17).

As shown later in the section on life history, the average age of the sockeye increased rather steadily in the returns from the broods spawned from 1919–43. This increase can be attributed chiefly to an increase in the proportion of smolts remaining an additional year or years in the lake prior to seaward migration. Speaking of this phenomenon Barnaby (1944, p. 293) says,

> The change in the period of time spent in fresh water is considered to be due to unfavorable environmental conditions, which may also adversely affect the survival value of the population.

According to his view, the fact that the smolts tend to remain longer in the lake is an indication of poor growing conditions, but the evidence may indicate the contrary.

Evidence that better growing conditions tend to cause migration of smolts at a later age is suggested by the older average age of the smaller year classes (figs. 48, 49, and 50) at Karluk. The excellent growing conditions that apparently exist especially for the smaller broods may be keeping the smolts in the lake for a longer period. The earlier age at migration of the Cultus Lake smolts, which encounter much less favorable growing conditions, might seem to support this view.

Against this explanation the fact is mentioned by Foerster (1944) that older smolts in the same brood are nearly always smaller (in this instance, third year fish) than younger smolts (second year fish) at the time the younger smolts leave the lake. It has been suggested, therefore, that there is a threshold size which must be attained before migration. We cannot fully subscribe to this hypothesis, but incline to the view (see appendix J for details) that migration is induced both by size and density of young. The threshold size for migration then will vary (within limits) inversely with the weight of the biomass of young.

Further confirmation of the inhibition of migration by too rapid growth is given by Foerster (1938, p. 186) who states,

> . . . there is evidence to indicate that the larger size of the latest groups of liberated fish, rather than weighting the data favorably by an abnormally high survival, affected them in opposite fashion by contributing to the nonmigration of individuals. It has recently been observed by Ricker (1938) and referred to in a previous paper (Foerster 1937a) that in some years at least, if not in every year, there occur in Cultus Lake certain populations of sockeye the individuals of which remain in the lake and mature. Specimens have been taken in small-mesh gill nets and have been found maturing in their second, third, or fourth years. These sockeye show distinct differences in color, size, habits, and sex ratio to the common landlocked sockeye (*O. nerka kennerlyi*) and Ricker has given to them the name "residual" sockeye.
>
> These "residual" fish, according to Ricker, are believed to result, in part, from normal young sockeye of anadromous stock which have experienced unusually rapid growth during their first or second years and do not respond to the migratory stimuli in the spring.

If the size-threshold to be attained before migration were not partially density-dependent, then there would be almost no smolt migration at Cultus Lake in years when young were abundant because the fish would be too small. Likewise in years of very low abundance practically all would migrate for the contrary reason.

If this hypothesis is correct, it offers a reasonable explanation at Karluk both for the older fresh-water age of the smaller year classes, and the trend toward an older fresh-water age in recent years as the size of the runs decreased. Furthermore, it would aid in keeping the smaller runs small and the larger runs large. The remedy

lies in increasing the number of young in the lake, either by larger escapements or by increasing survival of the young.

LIFE HISTORY OF THE KARLUK RIVER SOCKEYE

Before discussing further the meaning of the foregoing analyses there are certain aspects of the life history that should be examined to determine their bearing on population abundance. Since 1921 there have been extensive collections of some types of data and these have been studied from this viewpoint.

Seasonal occurrence of the runs

The details of determining the seasonal occurrence of the runs are given in appendix A. Figure 33 shows the normal curves of the occurrence of the run for three 10-year periods and for the 30-year period from 1921 to 1950, inclusive.

The curves show three modes. The first mode has always been clearly recognized, but the last two modes have usually been considered as only one. Thus Barnaby (1944) says:

> There is a definite mode in June, a minimum during the week ending July 12, followed by a second mode. The second mode itself is slightly bimodal; however, the data for any single year clearly show that the minimum occurs during the period of the week ending July 5 to the week ending July 19 and only one mode is present during the fall run. It appears that there are two distinct red salmon runs to the Karluk River each year, the spring run which reaches a maximum during June and the fall run which reaches a maximum between the last week of July and the first week of September.

Data for 10 years were available to Barnaby contrasted with that for 30 years at present. With this additional data, the point concerning the modes has become clear. Note that in figure 33 the fall run is bimodal in each of the three 10-year periods. The question concerning the presence of a lower minimum between the first two modes is largely a matter of the spacing of the modes. The first two modes are 7½ weeks apart and the last two 5 weeks apart. It is clear that these modes are not due to chance, so that if seasonal occurrence alone is to be used as a criterion for postulating separate populations one must postulate not two, but three populations. We will show later that these modes are caused by seasonal differences in age composition.

Age composition of the runs

Sockeye salmon of Karluk River vary considerably in age at maturity, returning at 3 to 8 years of age. Within each of these age groups there is a further differentiation according to the proportion of the time spent in fresh-water and marine environments. Although the bulk of the young leave the lake in the late spring of their third or fourth year of life (reckoning from the time of egg deposition) a few remain in the lake until their fifth year, some leave in their second year, and an undetermined number drop down the river to the sea during their first summer without any period in the lake. Likewise, the growing period at sea varies from part of one summer to four summers.

In the years for which ages of the run are analyzed, 1922 and 1924–49, 21 different combinations of fresh-water and ocean ages were read. Three combinations, 3_3, 5_1, and 5_5, occurred only

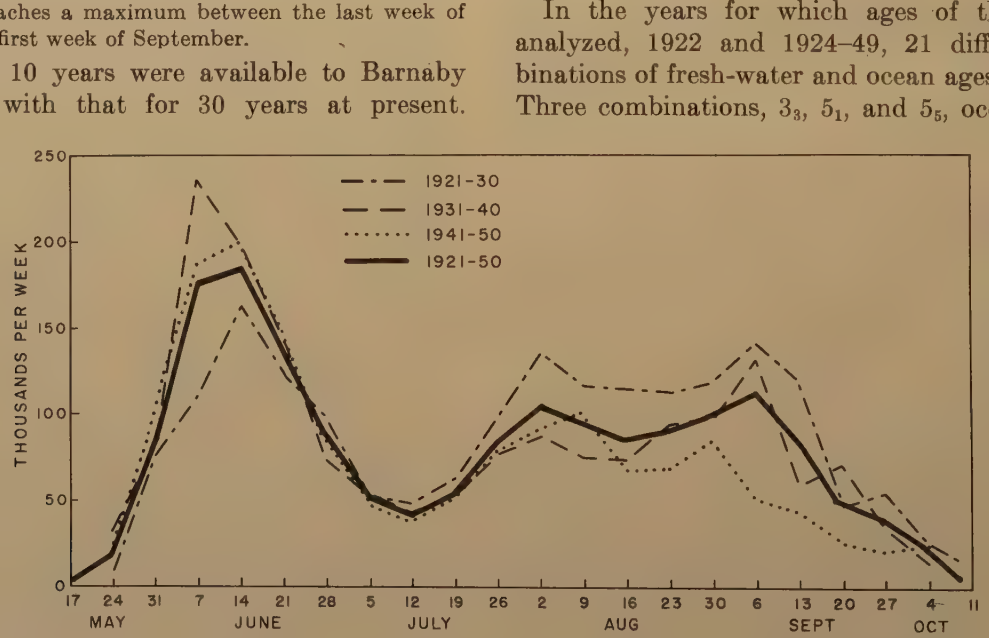

FIGURE 33.—Showing by weeks the normal seasonal run of sockeye entering the Karluk River by 10-year periods from 1921 to 1950.

ıce; 18 groups occurred more regularly. Ages e denoted by two figures, thus 5_3 means a fish turning to spawn in its fifth year, which migrated sea in the spring of its third year.

The details of determining the age composition the runs and the detailed tables are given in ppendix B.

elation of age of seaward migration and age at maturity with the season of return migration to the river

The seasonal occurrence of each age group is ther distinctive. Comparison of the different ge groups (tables A–3 and A–4, appendix) gives nvincing evidence that the time of the returning migration of each age group is governed by two factors: fresh-water age and ocean age. Except for the few adults that entered the sea as fry (3_1 and 4_1 groups) the age of downstream migration has a negative effect on the season of return; the 2-year migrants run first, followed by the 3-, 4-, and finally the 5-year migrants.

The ocean age, on the contrary, has a positive effect. The 4-ocean fish run earliest, followed in succession by the 3-, 2-, 1-, and 0-ocean groups. This is best seen in table A–4 which is on a cumulative basis.

The cumulative curves of percentage seasonal occurrence by weeks are shown in figures 34 to 38.

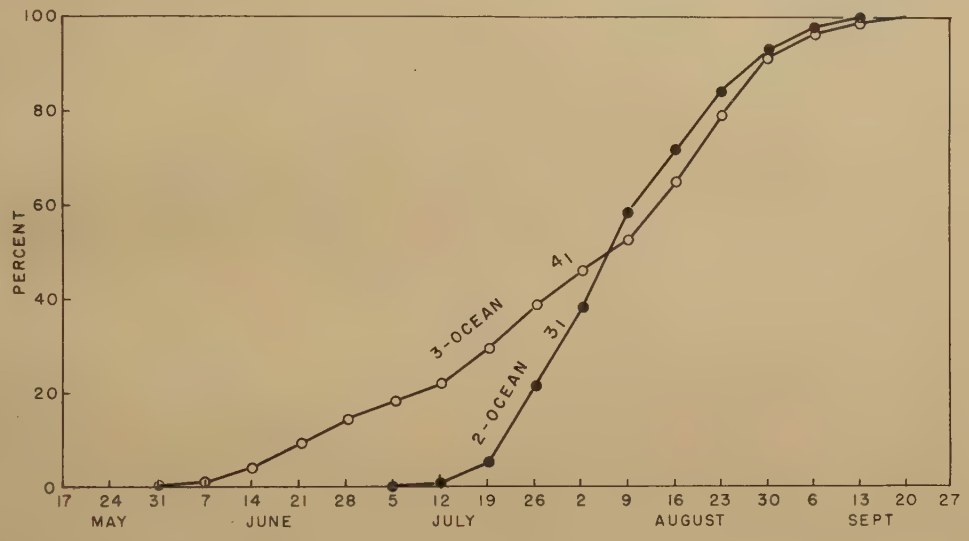

FIGURE 34.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 1-year-old seaward migrants.

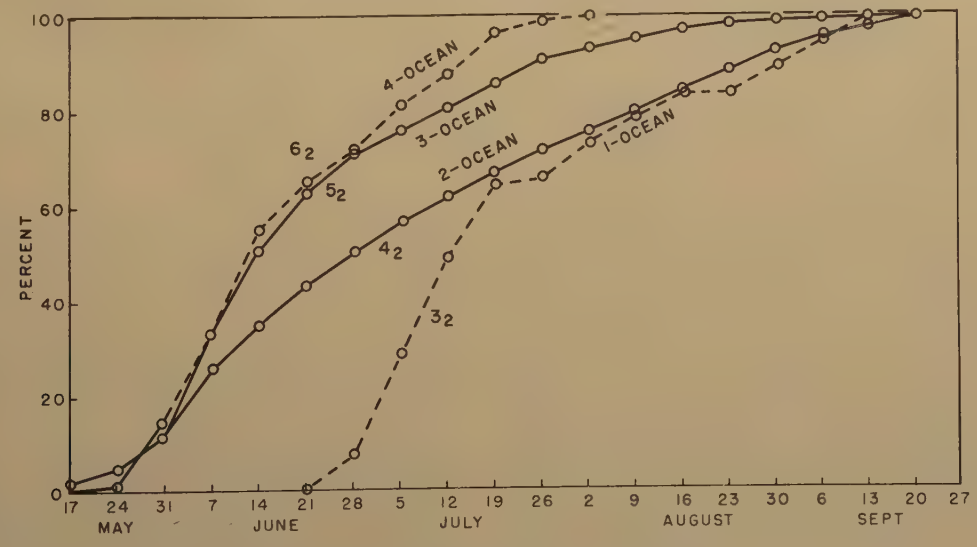

FIGURE 35.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 2-year-old seaward migrants.

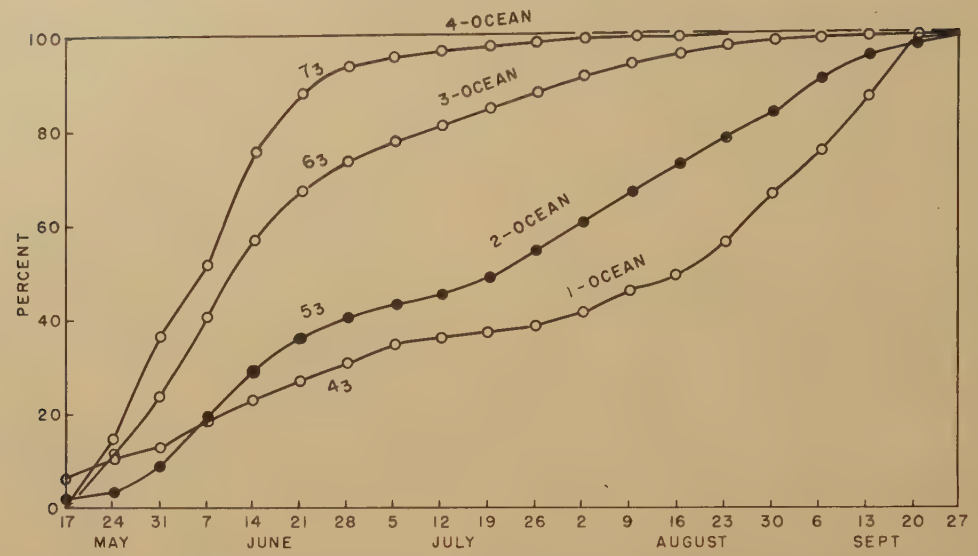

FIGURE 36.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 3-year-old migrants.

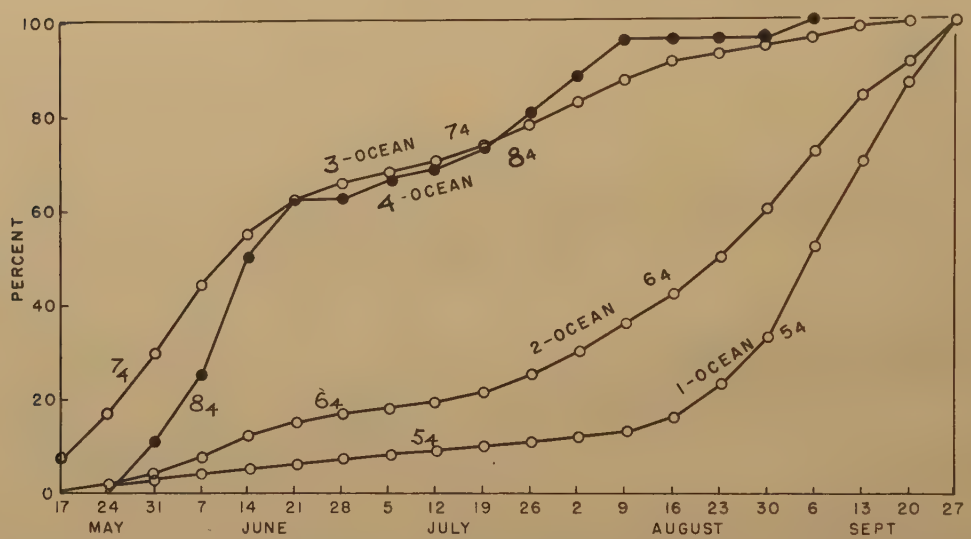

FIGURE 37.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 4-year-old migrants.

The effect of the time spent in the ocean on the season of return migration is very apparent. For each group of migrants, those that remained longest at sea migrated earliest in the season, and those spending the least time at sea migrated latest.

The relation of age at time of seaward migration on the seasonal period of returning migration of adults, irrespective of ocean age, is shown in figure 39 and table 16. In this table the number at each age is weighted according to the normal annual numbers of each age combination. Thus, the curve for migrant age 1 is composed of th curve (table 16) for the 3_1 group weighted by 93 and of the 4_1 group weighted by 1,675; the weigh employed for each age group are given in table 1

Only 8 of the 18 commonly occurring age com binations make any substantial contribution to th runs. These include all the groups in which th migrant age is 2 to 4 with the ocean age 1 to All groups are unimportant in which either th migrant age or the ocean age falls higher or low than these middle ranges.

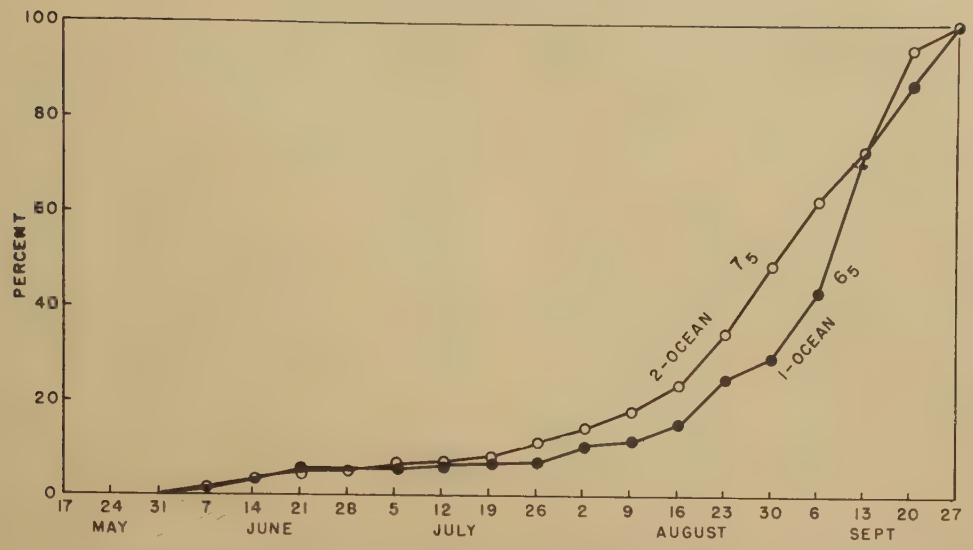

FIGURE 38.—Cumulative percentage seasonal occurrence by age at maturity of sockeye derived from 5-year-old seaward migrants.

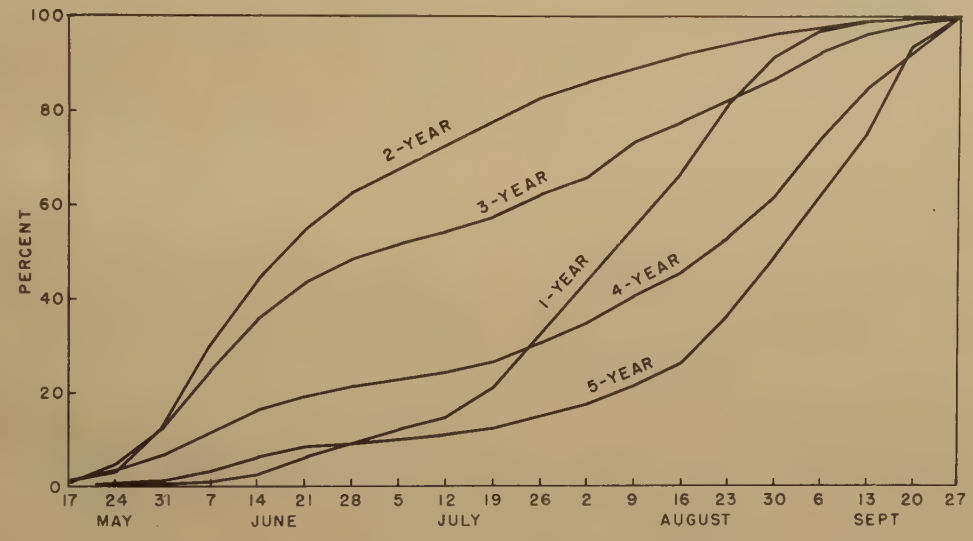

FIGURE 39.—Cumulative percentage seasonal occurrence by age at time of seaward migration of adult sockeye derived from 1- to 5-year-old seaward migrants.

The relation of the time spent at sea on the asonal period of the returning migration of ults, without regard to age at time of seaward gration, is given in table 18 and shown in figure

hen figure 39 is compared with figure 40, the posing effects of migrant age and ocean age on e seasonal occurrence are very obvious.

In order to show more clearly the effects of e on seasonal occurrence a multiple regression s calculated in which:

X_1 = Total age.
X_2 = Age at time of seaward migration.
Y = Percent of an age group accumulated by the end of the week ending on July 26.

The week ending July 26 was chosen as it represents the approximate midpoint of the runs (54 percent accumulated). Twelve age groups were used (table 17) omitting all with less than 1,000 fish and also the 4_1 group, as the 1-year migrants do not conform to the remainder of the runs. The totals for each group for July 26 are shown in table A4.

TABLE 16.—*Cumulative percentage occurrence of adults according to their age at time of seaward migration*

Week ending	Age at time of seaward migration				
	1	2	3	4	5
May 17	0.0	1.0	0.9	1.2	0.0
May 24	.0	2.9	4.8	3.1	.5
May 31	.2	12.1	12.3	6.2	1.2
June 7	1.0	30.1	24.6	11.6	3.6
June 14	2.9	43.9	35.9	16.3	6.6
June 21	6.4	54.3	43.7	19.6	8.6
June 28	9.7	62.2	48.4	21.7	9.4
July 5	12.2	67.6	51.5	23.1	10.1
July 12	14.7	72.5	54.0	24.5	11.1
July 19	21.3	77.9	57.2	26.8	12.4
July 26	33.0	82.6	62.1	30.4	14.7
Aug. 3	43.9	86.0	67.9	35.0	17.7
Aug. 9	55.3	88.8	73.4	40.4	21.2
Aug. 16	67.5	91.6	77.9	45.7	26.1
Aug. 23	81.2	94.0	82.3	52.9	36.1
Aug. 30	91.8	96.2	86.8	62.0	48.9
Sept. 6	97.0	97.6	92.3	74.0	61.7
Sept. 13	99.3	99.0	96.4	84.7	75.4
Sept. 20	100.0	99.9	98.5	92.3	94.0
Sept. 27	100.0	100.0	100.0	100.0	100.0

TABLE 17.—*Normal age distribution of annual run of sockeye, May 17 to September 27, for 1922 and 1924–49*

Age group	Number of fish	Total age	Number of fish	Migrant age	Number of fish	Ocean age	Number of fish
3_1	937	3	1,009	1	2,612	0	131
3_2	72						
4_1	1,675	4	38,457	2	38,125	1	51,592
4_2*	15,928*						
4_3*	20,723*	5	947,548	3	1,211,010	2	1,262,383
4_4	131						
5_2*	21,990*	6	640,636	4	423,571	3	363,906
5_3*	895,479*						
5_4*	30,079*	7	51,618	5	4,661	4	1,967
6_2	135						
6_3*	293,387*	8	711				
6_4*	346,396*						
6_5	718						
7_3	1,421						
7_4*	46,554*						
7_5	3,643						
8_4	411						
8_5	300						
Total	1,679,979		1,679,979		1,679,979		1,679,979

*Age groups contributing materially to the runs.

TABLE 18.—*Cumulative percentage occurrence of adul according to their ocean age*

Week ending	Ocean age at time of return				
	0	1	2	3	4
May 17	0.0	2.5	0.5	2.4	
May 24	.0	4.4	2.3	11.0	1
May 31	.0	6.8	7.6	22.1	2
June 7	.0	9.7	16.4	40.2	4
June 14	.0	12.5	24.6	55.7	6
June 21	.0	14.8	30.4	66.1	8
June 28	.0	16.9	34.0	72.2	8
July 5	.0	19.3	36.3	76.0	8
July 12	.0	20.3	38.5	79.0	9
July 19	.0	21.1	41.5	82.6	9
July 26	.0	22.5	46.4	86.2	9
Aug. 2	.0	24.1	52.6	89.9	9
Aug. 9	.0	26.7	58.8	92.9	9
Aug. 16	13.1	29.6	64.3	95.2	9
Aug. 23	26.2	36.8	70.2	96.8	9
Aug. 30	50.8	46.8	77.0	98.0	9
Sept. 6	66.9	61.5	85.6	98.8	10
Sept. 13	86.9	76.8	92.4	99.5	
Sept. 20	96.2	92.0	96.3	99.9	
Sept. 27	100.0	100.0	100.0	100.0	

The resulting correlations were $r_{12}=0.5$ $r_{y_1}=0.18$ and $r_{y_2}=-0.68$. The β coefficient however, give the measure of the relation each X to Y divorced from the effect of the oth factor:

$$\beta_{Y_{1.2}} = 0.88$$

$$\beta_{Y_{2.1}} = -0.88$$

$$\hat{Y}=17.67+24.37\ X_1-30.01\ X_2$$

The β-values show that migrant age and tot age have exactly equal and opposite effects determining the season of migration.

The effect of early migration on time of ru may be linked with the fact that those leavi the lake at the younger ages appear to be t

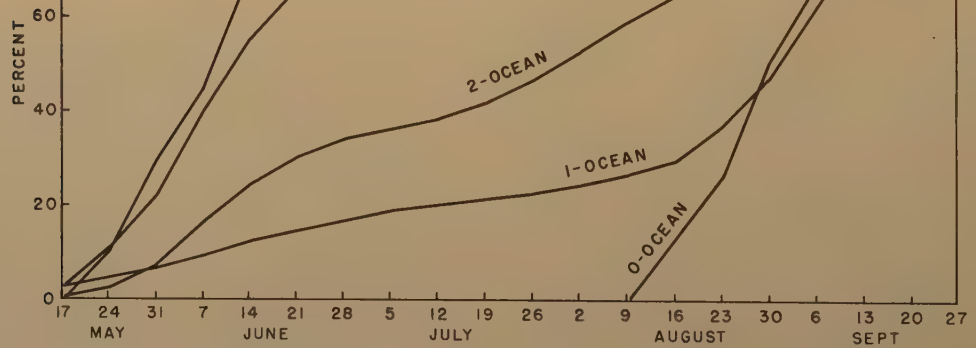

FIGURE 40.—Cumulative percentage seasonal occurrence by ocean age of adult sockeye derived from fish spending 0 to 4 seasons in the ocean.

stest-growing individuals of each brood. In ost organisms the age at maturity is closely lated to the rate of growth. Table 19 shows e relation between size and time of seaward gration. The season of seaward migration incides with the commencement of the period most rapid growth. Since the 3-year-olds are owing relatively faster than the 4-year olds, eir decrease in size is more masked by growth. he 4-year-olds clearly show that the largest dividuals of the group were first to leave the ke.

lation between season of smolt migration and ocean age

There is a definite relation between the time at nich the smolts migrate and the length of their ay in the sea. Barnaby (1944) gives data for arking experiments conducted on different dates 1932. In the second and fourth experiments e fish were marked by excision of the adipose d one pectoral fin. Since the results from these d a previous experiment in 1930 showed that e pectoral-marked fish suffered heightened ortality, we have omitted the second and fourth arkings. The first and third markings (15,000 h each) employed the adipose and right ventral elvic) and adipose and left ventral, respectively. The first lot (first experiment) was taken on May and 28; the second lot (third experiment), on ne 6, 7, 8, and 9. Thus, the two lots average days apart. The results are as follows:

Ratio of 2-ocean to 3-ocean fish in returns

Age at release	Marking dates		
	May 27–28	June 6–9	Both dates
3	2.46	1.37	1.76
4	2.94	1.95	2.41

It will be noted that the 4-year-olds tend to stay a shorter time at sea than the 3-year-olds (ratio of 2.41 against 1.76). There is a sharp decrease in the proportion of 2-ocean returns from the second lot. Since we have shown (table 19) that the larger smolts of each age are first to leave the lake, it becomes apparent that the fastest-growing smolts are first to reach maturity.

The 4-year-old smolts tend to compensate for their greater age at seaward migration by a shorter sea life than the 3-year-olds. Within the group itself the faster-growing also tend to mature earlier (fig. 41), as the ratio of 2- to 3-ocean fish in the lot that migrated seaward earlier.

Do the Karluk sockeye belong to one population?

This question deserves careful study and elucidation, because the system of regulation depends on the answer. The prevalent opinion that there are races depends chiefly on the knowledge that different races of sockeye are found in some large river systems, such as the Fraser, and these races traverse the main channel leading to the different tributaries at different seasons. There has also

TABLE 19.—*Lengths of seaward migrants by weeks as percent of length during week ending June 7*

Year	3-year-old migrants				4-year-old migrants			
	May 31	June 14	June 21	June 28	May 31	June 14	June 21	June 28
5		99.65				96.08		
6	100.48	99.33			100.84	95.94		
7		102.12	101.15			100.64	98.84	
8		98.85	96.93			99.15	96.10	
9	102.41	98.17			100.50	94.24		
0	98.46	103.66	101.18	98.40	100.37	101.56	97.24	90.40
1	99.16	100.45	98.54		102.60	96.79	94.74	
2	99.72	99.94	100.15	103.16	101.52	96.43	91.86	96.54
3	99.43	98.74		95.26	101.38	96.60		93.97
4	102.09		101.01		105.12		96.20	
5	99.72	99.23			99.80	96.87		
6	102.63	97.66			104.76	96.14		
7	98.83	99.33	97.82		100.40	99.76		
8	98.34	101.08	101.41		97.77	98.69	97.85	
9		100.16	99.15			96.36	92.51	
0	99.09	98.18			102.60	97.33		
1	101.11	96.29			102.60	100.22		
7	98.24				100.16			
8	98.66		96.08		96.45		101.37	
9		97.05				98.47		
0	100.68	99.58	101.69	103.64	99.63	98.09	98.75	98.31
ms	1,599.05	1,789.47	1,095.11	400.46	1,616.50	1,759.36	965.46	379.22
ms	16	18	11	4	16	18	10	4
erage	99.94	99.42	99.56	100.12	101.03	97.74	96.55	94.81

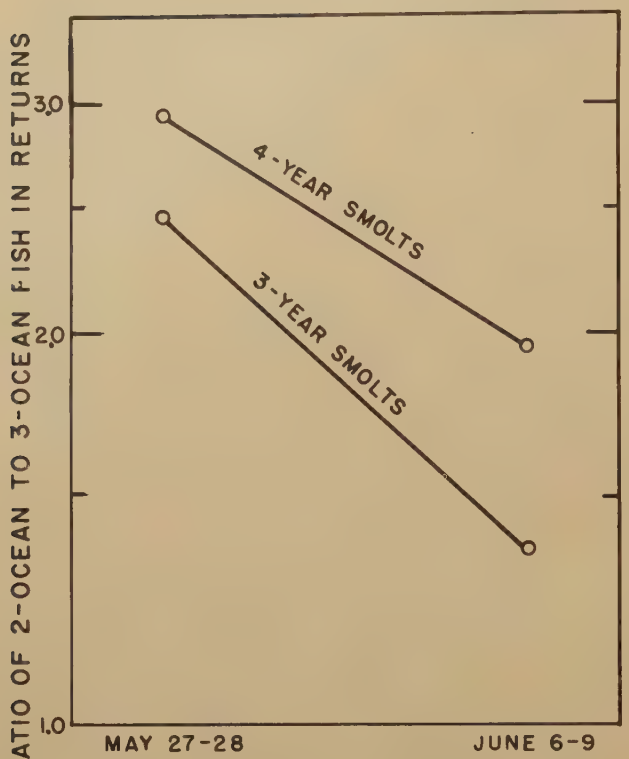

FIGURE 41.—Relation of season of smolt migration on the ocean age of the returning adults.

been a strong indication that at least two races may exist in the Chignik River, which enters Shelikof Strait from the mainland on the opposite shore from Karluk. However, neither the Fraser nor the Chignik present the same picture as Karluk.

The main Fraser constitutes merely a passageway for the salmon bound to particular lake systems. The question of two or more populations in a single lake as at Karluk is not involved. The Fraser salmon are predominately of one age so that the problem of varying age at maturity affecting the season of migration does not arise.

The Chignik system contains two large lakes, one deep oligotrophic lake on the southern side of the Alaska Peninsula, and one shallow eutrophic lake on the northern side of the peninsula so that two races, each growing in a different ecological situation are possible.

Let us examine for the Karluk system the available evidence for and against the existence of different races. The basis for the hypothesis of two races is the shape of the curve for the seasonal occurrence of the run and the fact that surveys of the spawning grounds seem to indicate a pronounced midsummer lull in spawning activity. There also is some evidence that whereas the earlier spawners use all of the streams entering the lake, the later spawners use chiefly the larger streams and the lake itself. None of these facts, however, necessarily have any bearing on whether there is more than one self-perpetuating race of sockeye in the lake.

Before examining contrary evidence we might briefly examine the above facts to see whether they can be consistent with a single population. First, let us look at the curve of seasonal occurrence (fig. 33). This indicates two or possibly three distinct modes, and as the data cover a 30-year period there is no reason to doubt their authenticity. The curves of occurrence by age groups (table A3) show that there are not two but three distinct modes in both the 5_3 and 6_4 age groups, other age groups show at least one or two of the same three modes. If races are to be postulated on the shape of the curve of seasonal occurrence alone, we must admit of three rather than two populations.

A lull in the seasonal run to the river for one or more age groups of the population is not sufficient evidence of more than one population. There are many other explanations. One of these is the fact that those fish of an age group that are fully mature at the beginning of the season hasten to the river, causing a heavy initial run. This explanation is supported by the fact that those age groups with a long sojourn at sea run early in the season, their run corresponding with the early maturing 5_3 and 6_4 fish, while age groups with a short sojourn at sea run late in the season since they require additional summer growth to attain maturity.

The evidence for only one population of sockeye at Karluk is rather conclusive. In figures 42 to 45 are shown as percentages by weeks the seasonal occurrence of the runs of several age groups.

It will be noted in each instance that the 1-ocean-age fish, 3_2, 4_3, 5_4, and 6_5 ran latest in the season. Of this group the ones with the shorter fresh-water sojourn ran earlier, being the faster growing smolts. The 2-ocean-age fish, 4_2, 5_3, 6_4 and 7_5, ran earlier than the 1-ocean fish, and as in the 1-ocean group, the order of their abundance in relation to the season was governed by their fresh-water history. Thus the 4_2 fish ran pre-

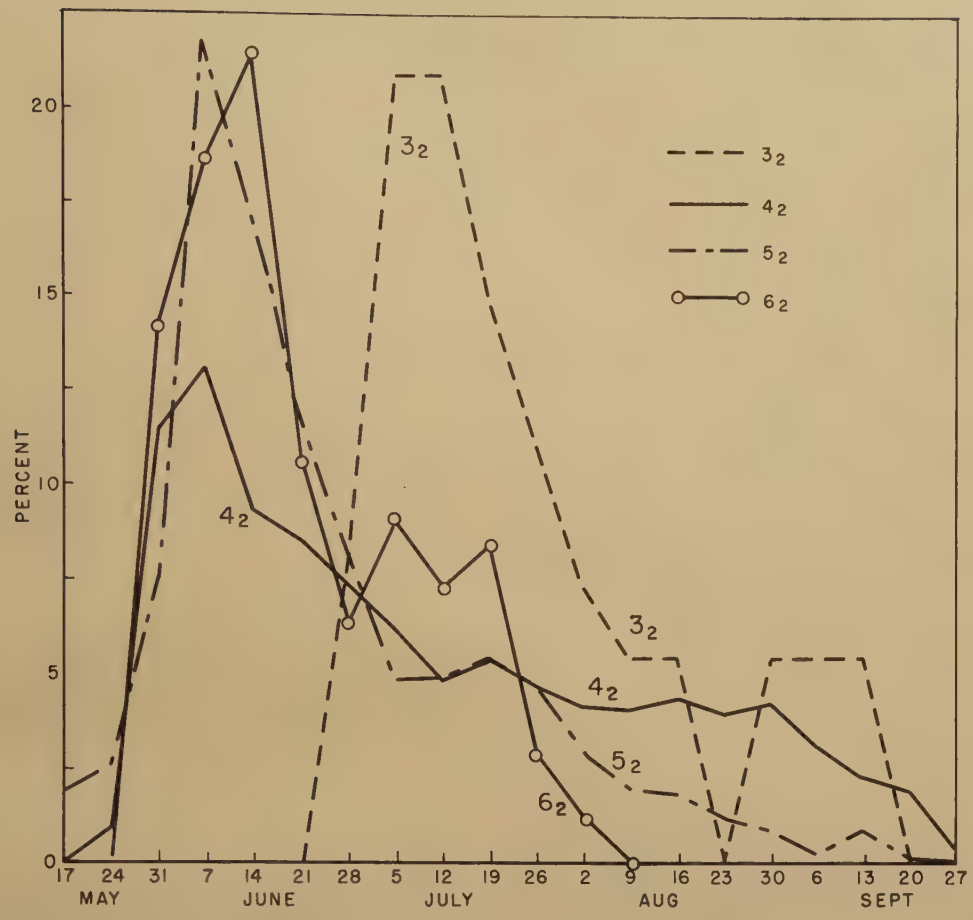

FIGURE 42.—Percentage frequencies of seasonal occurrence by age at maturity of sockeye derived from 2-year-old seaward migrants.

dominantly in the early summer attaining 50 percent by the week ending on June 28. The 5_3 group averaged 3 weeks later (48.9 percent by July 19), followed 5 weeks later by the 6_4 fish (50.5 percent by Aug. 23) and ending with the 7_5 group (49.3 percent by Aug. 30).

The same sequence of events holds true for the 3- and 4-ocean-age groups. These seasonal age relations show that the season of migration is linked with age, not with race.

If the runs were to consist of two populations, the spring (and early summer) and the fall (and late summer) portions of the runs would, of course, vary independently. However, the reverse is the case. The number of 4_3 fish (reference to figure 43 will show run predominantly in the fall) is highly correlated with the number of 5_3 fish running the following year, $r=.956$, which is highly significant (table 20).

TABLE 20.—*Correlations between adults of the same brood year from smolts descending to the sea in their third year, but returning at different ages*

X	Y			
	5_3	6_3	7_3	5_3+6_3
4_3	.956**	−.100	−.172	.909**
5_3		.006	−.182	
6_3			.716**	

The 5_3 age group always comprises the largest share of the runs. It is also the only age group that runs strongly during both spring and fall. To test the relationship of the spring and fall components of this run the group has been divided into two portions: those running before July 19 and those running later (table 21).

Since the variance was correlated with the mean in these series, the data were transformed to

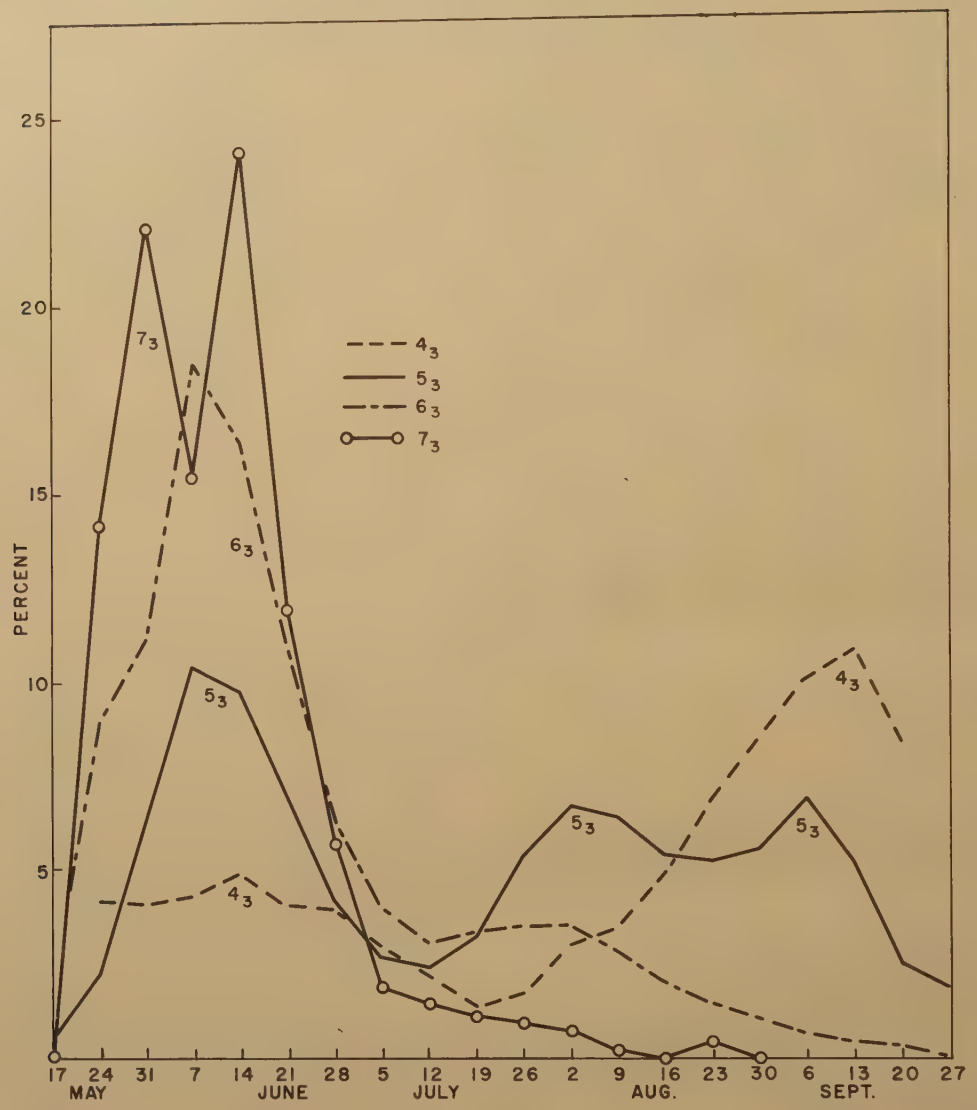

FIGURE 43.—Percentage frequencies of seasonal occurrence by age at maturity of sockeye derived from 3-year-old seaward migrants.

logarithms. Plots of temperature data showed that there is a positive relation between temperature and the proportion of 5_3 fish returning in the fall. Therefore, a multiple correlation was calculated to show the relation between the late-running 5_3 fish, Y, the early-running 5_3 fish, X_1, and the sum of the degrees of temperature (air) for Kodiak above 40° F, during July and August, X_2, the results are as follows for 1924–49 (except 1941 for which July temperatures were not available):

Logarithm of number of late-running 5_3 fish	Logarithm of number of early-running 5_3 fish	Accumulated monthly air temperature over 40° F at Kodiak during July and August
Y	X_1	X_2
Correlation of Y with X's	0.81854**	0.28461
Standard regression of Y on X's	.8071**	.2472

This indicates that about 64 percent of th variation in numbers of late-running 5_3 fish i associated with variations in the numbers o early-running 5_3 fish of the same brood.

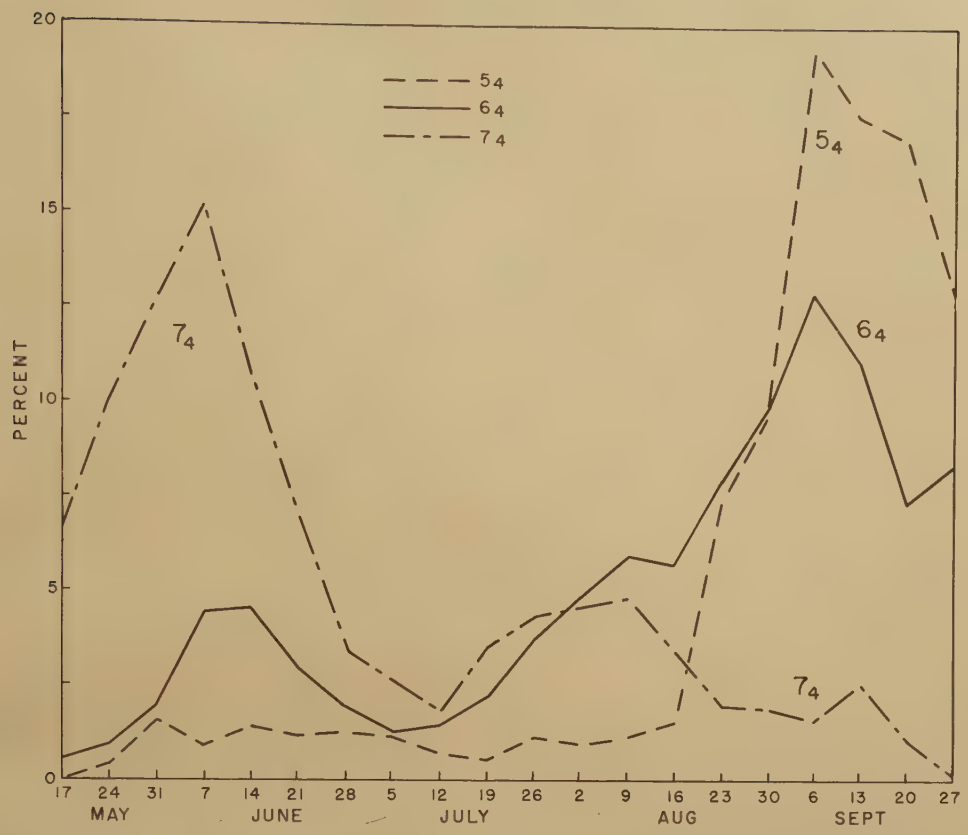

FIGURE 44.—Percentage frequencies of seasonal occurrence by age at maturity of sockeye derived from 4-year-old seaward migrants.

TABLE 21.—*Numbers of sockeye of age 5_3 occurring early and late in the season*

Year	Numbers in the run			Dates of occurrence of percentiles of run				
				Total run			Early run	Late run
	Early run (to July 19, in thousands)	Late run (after July 19, in thousands)	Total run [1] (thousands)	25th	50th	75th	50th	50th
922	132	560	692	July 27	Aug. 22	Sept. 7	June 25	Aug. 30.
924	676	716	1,393	June 15	July 26	Aug. 25 ca	June 14	Aug. 21.
925	629	1,357	1,985	June 26	Aug. 2	Aug. 24	June ?	Aug. 15.
926	1,469	2,491	3,960	June 17	Aug. 4	Aug. 26	June 6	Aug. 21.
927	627	513	1,140	June 12	July 6	Aug. 4	June 13	Aug. 10.
928	533	674	1,206	June 16	July 27	Aug. 13	June 10	Aug. 12.
929	170	216	386	do	July 23	Aug. 16	June 14	Aug. 14.
930	251	417	668	June 13	July 29	do	June 10	Aug. 11.
931	239	552	741	July 6	Aug. 5	Aug. 25	June 16	Aug. 21.
932	499	251	751	June 8	June 22	July 29	June 12	Aug. 9.
933	611	369	979	June 7	June 18	Aug. 9 ca	June 11	Aug. 9 ca.
934	409	303	712	do	June 28	Aug. 20 ca	June 9	?
935	256	248	504	June 10	July 14	Aug. 8	June 10	Aug. 10 ca.
936	659	1,050	1,708	June 17	July 30	Aug. 25	June 12	Aug. 20 ca.
937	1,178	412	1,589	June 7	June 17	July 22	June 11	Aug. 23.
938	784	543	1,326	June 10	June 26	Aug. 14	do	Aug. 25.
939	177	181	358	June 16	July 20	Aug. 16 ca	June 16	Aug. 26 ca.
940	238	181	419	June 4	July 6	Aug. 10	June 9	Aug. 14.
941	265	570	835	June 17	Aug. 7	Aug. 26	June 2 ca	Aug. 22.
942	356	245	601	June 10	July 3	Aug. 6	June 13	Aug. 18.
943	590	359	950	June 11	June 28	Aug. 22 ca	June 16	?
944	364	432	796	June 13	July 22	do	June 11	Aug. 18 ca.
945	181	82	264	June 9	June 22	July 27	June 13	Aug. 6 ca.
946	64	58	123	June 12	July 11	Aug. 8	June 16	Aug. 10.
947	64	94	158	June 21	July 26	Aug. 7	do	Aug. 5.
948	614	388	1,003	June 8	July 3	July 29	June 12	Aug. 2.
949	250	346	596	June 15	July 24	Aug. 7	do	Aug. 6.

[1] Slight discrepancies due to rounding off figures.

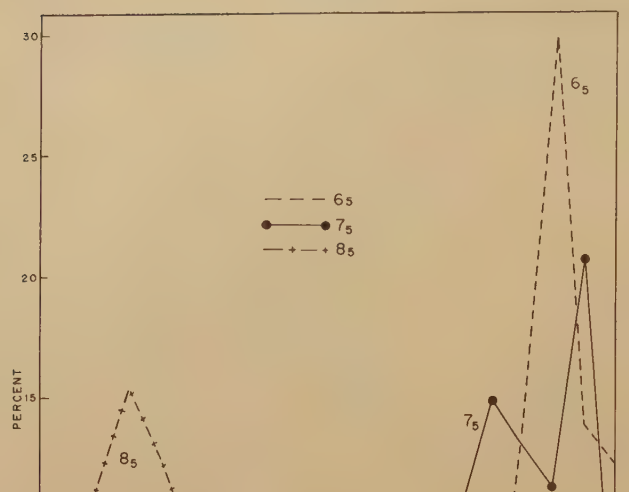

FIGURE 45.—Percentage frequencies of seasonal occurrence by age at maturity of sockeye derived from 5-year-old seaward migrants.

So far we have shown that grilse of 4_3 age (running chiefly in the fall) are undoubtedly of the same population as the fish of the 5_3 age group returning in the following year and running strongly during both spring and fall. Also a strong correlation has been found between the spring and fall-running fish of the 5_3 group.

Some of the smolts leaving the lake in their third year also return as the 6_3 and 7_3 age groups. The 7_3 group is so minor (table A-5) that it can safely be ignored, but the 6_3 group is the third largest, exceeded only by the 5_3 and 6_4 groups.

Because of the numerical importance of this 6_3 age group, and the fact that its members run chiefly in the spring (84 percent normally enter the river before July 19), it could conceivably be argued that it constitutes a separate and self-perpetuating population. Of course, in order for this to be true its members would have to either spawn apart from sockeye of the 5_3 age group or (which would seem highly improbable) seek out individuals of the same age group with which to spawn. Although either alternative seems too improbable to warrant serious consideration we shall examine the evidence pro and con.

The total numbers of the 6_3 group are not significantly correlated with the total numbers of the 5_3 group of the previous year, r equals .006 or with the 4_3 group of the same year class, r equals —.100. However, there are sound biological reasons why these correlations of total numbers are not expected to be significant. The number of 6_3 fish is dependent both on the total number of survivors of the brood year and on the number that mature at an earlier age, so that when a high proportion of 3 fresh-water fish of a brood mature in their fifth year, there are fewer remaining to mature in their sixth year.

To show the relation between brood size and the proportion maturing in their sixth year, the percentage of each brood year (1920–42 brood years) returning as 6_3 fish has been correlated with the total numbers of the same brood year returning at all ages. The correlation coefficient of —.5567 while not denoting a high degree of relationship is highly significant. The explanation of this relationship may be twofold. First the number of survivors may be greater from brood years with faster-growing (and therefore larger) smolts. When fish are larger they tend to return at younger ages, resulting in a lesser percentage of 6_3 fish from brood years producing large runs. Secondly, there is undoubtedly a significant natural mortality during the additional year in the sea so that when a smaller percentage of a brood remain at sea until their sixth year, the total number ultimately returning to the river is greater.

There is, however, a significant relation between the 6_3 and the *late-running* 5_3 fish that is somewhat obscured by other factors. To remove the effect of these factors in order to determine the degree of relationship it was first necessary to obtain two sets of residuals. The first set, for the 6_3 fish, are the residuals (which we will call set A) from the regression of the percent that the 6_3 fish were of the total of each brood year of smolts migrating to sea in their third year, on the total numbers of returning adults in each brood year. The second set (which we shall call set B) for the late-run 5_3 fish, are the residuals from the regression of the logarithms of the late-run 5_3 fish on the logarithms of the early-run 5_3 fish with the temperature factor held constant.

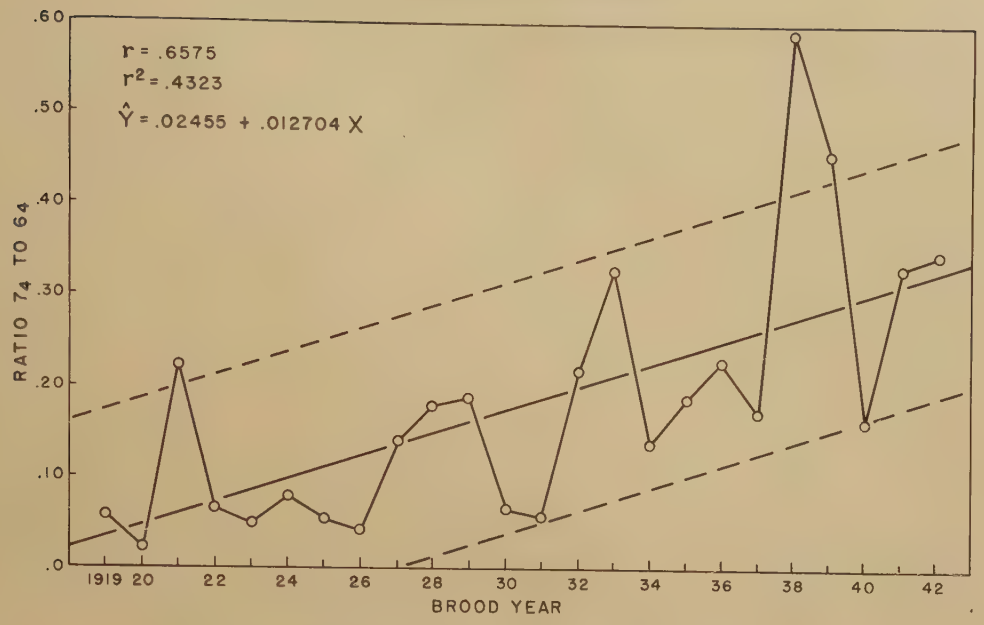

FIGURE 46.—Regression of the ratio of 7_4 to 6_4 of the same brood on time.

The coefficient of correlation between the residuals of set A and set B, −0.5045 is statistically significant at the 5 percent level. This indicates two things: first, that the 5_3 and 6_3 fish belong to the same population, and second, that the fluctuations in the numbers of 6_3 fish are determined chiefly by the fluctuations in rate of growth of the 3-freshwater age group.

In summary, the evidence strongly indicates that the Karluk sockeye salmon comprise one population, since the number of fish of the same brood running at different seasons, and even in different years, are significantly correlated.

Increase in average age at maturity

Barnaby (1944) pointed out that there seemed to be an increase in age of the sockeye from the brood years of 1920–29. He concludes that since the evidence from his marking experiments does not indicate any marked change in the ocean mortality of either the 3-year or the 4-year seaward migrants, the change may be due to an increase in the length of fresh-water residence. He further suggests that this may be linked with a decreased rate of growth in fresh water.

To test this theory over a longer period of time the proportion of 7_4 age fish to the 6_4 age fish of the same brood was correlated with time for the brood years of 1919–42 (24 years). The correlation coefficient of +0.658 is highly significant. The average ratio of $7_4/6_4$ rose from 0.03 for the 1919 brood to 0.33 for the 1942 brood (fig. 46).

The same correlation was tried using only the late-running 6_4 fish (running after July 19) and the correlation coefficient was +0.761. This indicates clearly that the number of spring-running 7_4 fish is closely correlated with the numbers of fall-running 6_4 fish. As the ratio appeared to fluctuate more widely as its value increased the logarithm of the 7_4/late-running 6_4 ratio was correlated with time resulting in a correlation coefficient of +0.812 (fig. 47). The antilogs of the regression line show an increase from .05 to .54 in the 7_4/late-running 6_4 ratio between the 1919 and 1943 brood years (fig. 47).

That increasing age of seaward migrants is a general phenomenon and not connected with one age group of seaward-migrating smolts is shown by the correlation coefficient of +0.579 between the ratio of 6_3 fish to late-running 5_3 fish against time.

Having established that the average duration of lake residence, as shown by the seaward-migrant ages of the returning adults, has increased steadily and markedly over a period of 24 years, we shall next inquire into the underlying cause.

Relation of size of brood to age at maturity

Since the increase in average age of the adult sockeye has been occurring during a period when

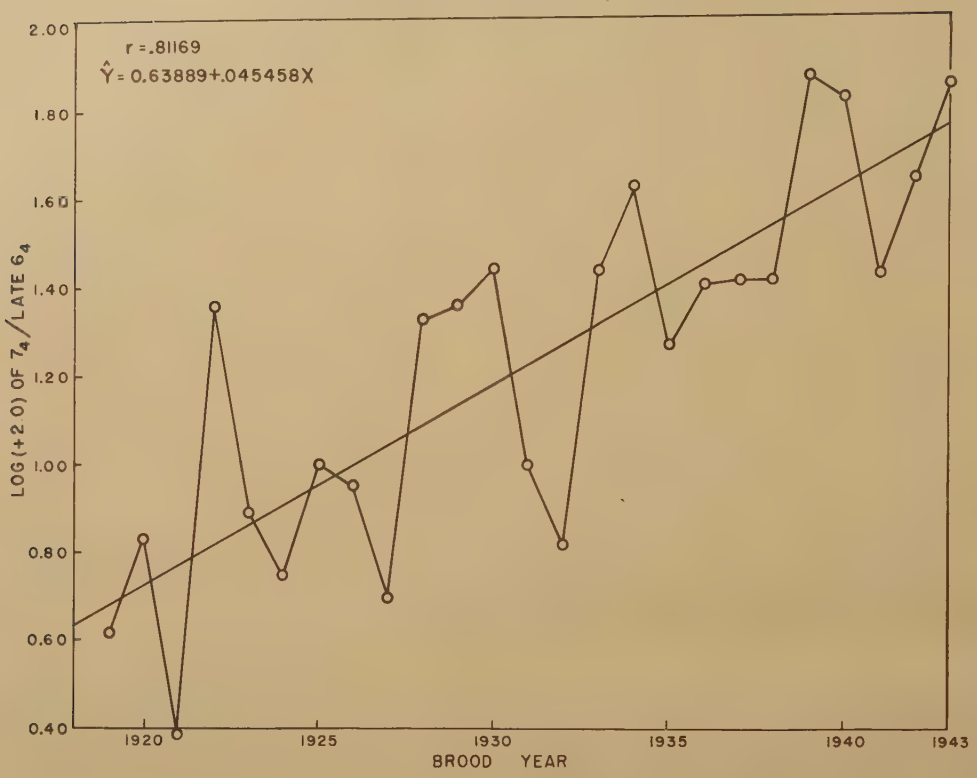

FIGURE 47.—Regression of log of ratio of 7_4 age fish to late-running 6_4 sockeye of the same brood on time.

the runs are declining in size, one should therefor inquire whether there is any relation between age at maturity and size of the brood. In table 22 we have shown the percentage of 4, 5, 6, and 7-year-olds in each of the 23 broods from the spawning of the years 1920–42, inclusive. The coefficients of correlation of age percentage on brood-size are:

Age at maturity	Coefficient of correlation
4 (plus a few 3)	0.26
5	.78**
6	−.78**
7 (plus a few 8)	−.60**

The regressions of age percentage on brood size are shown in figures 48 and 49, and all four curves are combined in figure 50. The linear regressions obviously do not give the best fit if the curves are extrapolated for larger broods. In fact, table 23 shows clearly that for larger broods linear extrapolation would yield more than 100 percent. Therefore in figure 50 and the bottom portion of table 23, it was necessary to make empirical curvilinear fits from grouped averages, for all but the 4-year-olds.

TABLE 22.—*Percent at certain ages in returns from brood years*

Brood year	Total returns (−000)	Percent at each age			
		[1] 4	5	6	[2] 7
1920	2,849	2.03	72.35	25.16	0.46
1921	4,494	4.31	89.45	5.54	.69
1922	2,282	6.62	55.99	36.48	.91
1923	1,990	2.76	61.08	35.24	.91
1924	809	2.01	48.72	47.27	2.01
1925	1,607	.73	50.52	45.73	3.02
1926	1,461	2.82	57.89	37.15	2.14
1927	1,618	1.69	48.76	45.34	4.21
1928	2,630	1.22	39.22	54.11	5.45
1929	1,587	1.12	51.00	42.27	5.61
1930	1,172	5.87	50.72	39.80	3.61
1931	2,578	4.75	71.22	22.18	1.86
1932	2,538	2.45	65.25	28.87	3.43
1933	2,186	2.99	62.35	32.01	2.66
1934	1,261	5.68	33.11	56.19	5.02
1935	1,250	.78	38.90	53.23	7.09
1936	1,353	1.15	65.11	28.85	4.90
1937	1,334	1.50	46.57	48.23	3.70
1938	1,587	2.25	61.98	30.58	5.20
1939	1,831	1.89	46.95	46.10	5.06
1940	858	1.86	45.69	48.67	3.78
1941	575	2.71	26.66	58.94	11.70
1942	607	1.18	32.95	53.81	12.06

[1] Plus a few 3-year-olds.
[2] Plus a few 8-year-olds.

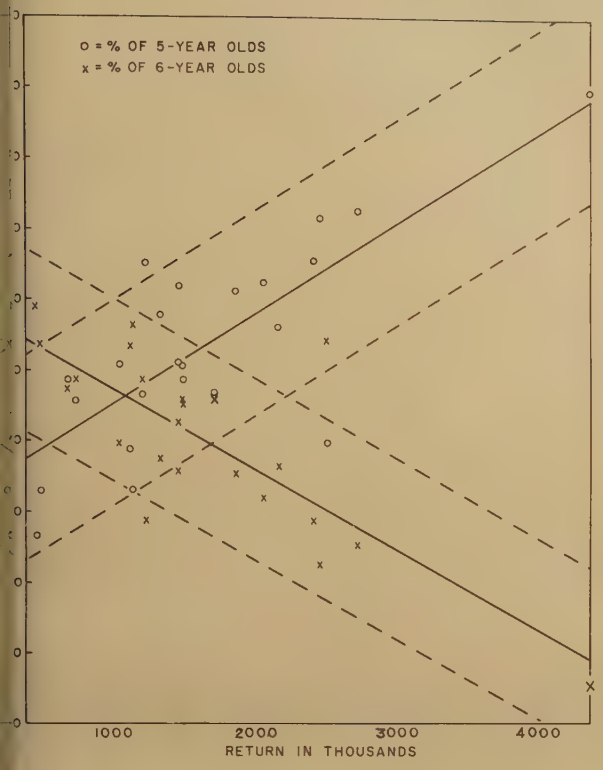

FIGURE 48.—Regressions of percent of 5-year-olds and of percent of 6-year-olds on the size of the returning brood of which they are a portion.

The relation of brood size to age percentage may be easily converted to average age for each brood size from table 23. Thus during the period 1922 and 1924–49 (table 16) the average run of 1,680,000 sockeye averaged 5.42 years in total age, which compares closely with 5.41, the average age calculated from table 23 for a run of 1,700,000. The average calculated ages for runs of 500,000 to 4,000,000 are:

Size of run	Average age
500,000	5.69
1,000,000	5.58
1,500,000	5.49
2,000,000	5.41
2,500,000	5.26
3,000,000	5.15

This negative relation between average-age and brood-size is caused primarily by the young of the smaller broods tending to remain an additional year in the lake (p. 136).

Seasonal distribution of the escapement

The seasonal distribution of escapement has not paralleled the seasonal occurrence of the runs.

TABLE 23.—*Curves for estimating ages of Karluk sockeye in returns of varying size*

Number in returns (−000)	Percent at each age by linear least square fit				
	4	5	6	7	Total
0	1.73	30.48	60.04	7.75	100.00
1,000	2.24	43.37	48.69	5.71	100.01
2,000	2.75	56.26	37.34	3.66	100.01
3,000	3.26	69.14	25.99	1.61	100.00
4,000	3.76	82.03	14.64	−.43	100.00
5,000	4.00	95.00	3.00		
6,000	4.30	100.00			
	Percent at each age by empirical fit from grouped averages				
0	1.7	25.5	62.8	10.0	
250	1.8	30.5	58.7	9.0	
500	2.0	35.0	55.0	8.0	
750	2.1	39.3	51.6	7.0	
1,000	2.2	43.5	48.2	6.1	
1,250	2.4	47.0	45.3	5.3	
1,500	2.5	50.4	42.3	4.8	
1,750	2.6	54.1	39.2	4.1	
2,000	2.8	57.0	36.7	3.5	
2,250	2.9	60.0	34.1	3.0	
2,500	3.0	63.0	31.4	2.6	
2,750	3.2	65.9	28.8	2.1	
3,000	3.3	68.7	26.3	1.7	
3,250	3.4	71.2	24.0	1.4	
3,500	3.5	73.6	21.6	1.3	
3,750	3.6	76.1	19.2	1.1	
4,000	3.8	78.2	17.0	1.0	
4,250	3.9	80.3	15.0	.8	
4,500	4.1	82.2	13.1	.6	
4,750	4.2	84.1	11.3	.4	
5,000	4.4	85.8	9.5	.3	
5,250	4.5	87.4	7.9	.2	
5,500	4.6	88.8	6.4	.2	
5,750	4.7	90.1	5.1	.1	
6,000	4.9	91.2	3.9	.0	
6,250	5.0	92.0	3.0		
6,500	5.2	92.7	2.1		
6,750	5.3	93.3	1.4		
7,000	5.4	93.8	.8		
7,500	5.8	93.9	.3		
8,000	6.0	94.0	.0		

This is similar to conditions on the Fraser River (Rounsefell and Kelez, 1938, pp. 764–765) where the fishing during the early years was concentrated on the peak of the run with the result that this portion was depleted early in the history of the fishery. The total runs, catches, and escapements for the 30-year period from 1921 to 1950 are given in tables 24, 25, and 26. The tendency for low escapements during the middle of the season and high escapements both early and late is very marked.

The percent of the run escaping by time periods is given in table 27 and figure 51. This arouses the question of whether the central portion of the run has declined more than the early and late portions. If each portion were to represent a more or less separate and self-sustaining population such a tendency should show. However, if the entire run is one population with the time of seasonal run determined largely by varying ecological conditions to which each brood is subjected, then all portions should show the same general trends.

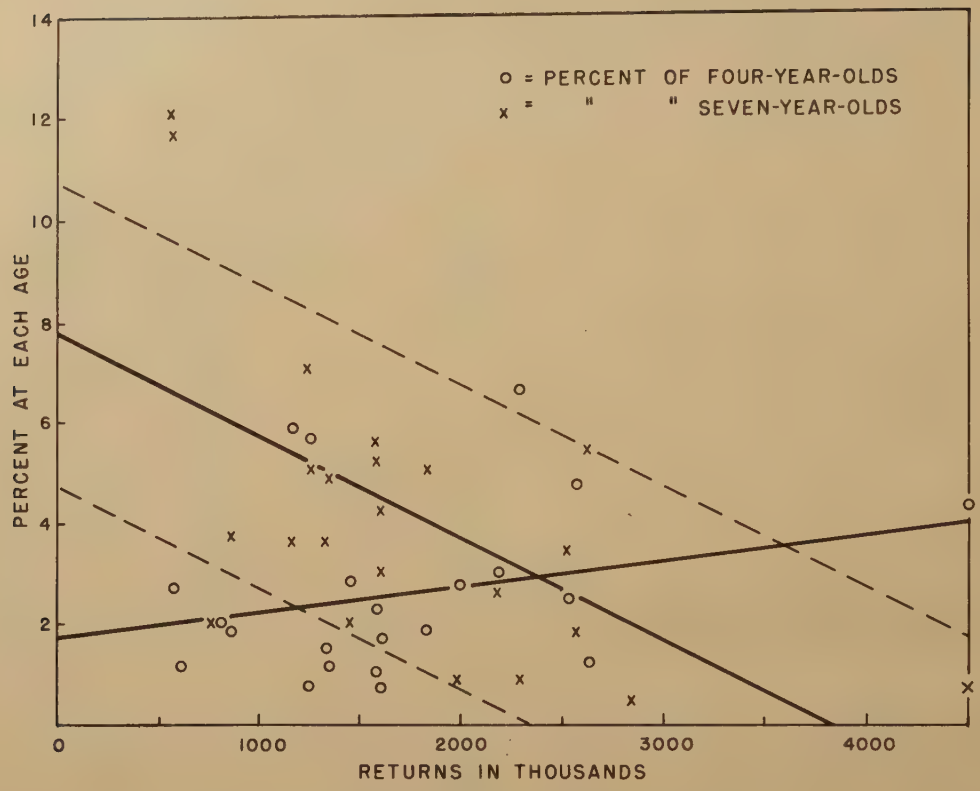

FIGURE 49.—Regressions of percent of 4-year-olds and of percent of 7-year-olds on the size of the returning brood of which they are a portion.

TABLE 24.—*The total run of sockeye to the Karluk River, 1921 to 1950*

Year	Total run by periods in thousands							
	to May 31	June 1 to June 21	June 22 to July 19	July 20 to Aug. 16	Aug. 17 to Sept. 13	Sept. 14 to end of season	Aug. 17 to end of season	Total run
1921	22	523	589	932	847	230	1,077	3,143
1922	10	135	200	216	395	102	497	1,058
1923	73	275	206	407	370	94	464	1,425
1924	91	457	314	349	?	?	742	1,953
1925	63	536	276	954	876	239	1,115	2,944
1926	561	845	466	1,138	1,773	137	1,910	4,920
1927	62	517	256	402	268	82	350	1,587
1928	166	587	335	598	320	89	409	2,095
1929	76	310	117	229	309	87	396	1,128
1930	44	287	149	337	253	184	437	1,254
1931	63	289	190	338	561	184	745	1,625
1932	49	432	207	273	274	177	451	1,412
1933	27	757	296	305	357	71	428	1,813
1934	204	893	288	316	?	?	669	2,370
1935	162	548	168	294	227	132	359	1,531
1936	183	603	283	613	675	96	771	2,453
1937	5	1,087	345	298	507	94	601	2,336
1938	0	938	285	396	?	?	595	2,214
1939	84	455	227	189	209	51	260	1,215
1940	269	303	104	229	?	?	363	1,268
1941	226	289	102	367	?	?	645	1,629
1942	153	289	151	195	284	64	348	1,136
1943	155	675	290	163	?	?	444	1,727
1944	99	503	173	294	?	?	341	1,410
1945	60	702	254	217	89	13	102	1,335
1946	65	248	136	104	39	78	117	670
1947	5	219	69	176	119	7	126	595
1948	179	449	265	424	86	8	94	1,411
1949	34	380	162	397	162	6	168	1,141
1950	48	460	170	267	270	48	318	1,263
Sum	3,238	14,991	7,073	11,417	-------	-------	15,342	52,061
Minus 1924 and 1934	2,943	13,641	6,471	10,752	-------	-------	13,931	47,738

TABLE 25.—*The total catch of Karluk River sockeye, 1921 to 1950*

Year	Total catch by periods in thousands						
	to May 31	June 1 to June 21	June 22 to July 19	July 20 to Aug. 16	Aug. 17 to Sept. 13	Sept. 14 to end of season	Total
1921	0	35	394	591	567	56	1,643
1922	0	40	102	175	318	23	658
1923	0	141	126	254	199	10	730
1924	0	116	180	139	?	?	891
1925	0	42	151	663	467	0	1,323
1926	0	235	317	773	1,050	12	2,387
1927	0	34	180	310	191	0	715
1928	0	110	201	469	195	26	1,001
1929	0	57	83	87	0	0	227
1930	0	1	103	50	2	1	157
1931	0	106	147	189	243	67	752
1932	0	159	157	215	143	0	674
1933	0	403	158	193	65	7	826
1934	0	371	249	?	?	?	919
1935	0	280	157	175	43	0	655
1936	0	348	199	531	0	0	1,078
1937	0	300	259	227	285	0	1,071
1938	0	206	190	354	234	0	984
1939	0	209	179	114	2	5	509
1940	0	13	62	201	155	20	451
1941	0	152	52	231	259	5	699
1942	0	134	106	127	139	1	507
1943	0	280	215	106	204	0	806
1944	0	266	154	221	0	0	641
1945	0	349	203	109	15	0	676
1946	0	36	96	96	0	0	228
1947	0	31	22	55	2	0	110
1948	0	104	222	330	1	0	657
1949	0	73	114	263	0	0	450
1950	0	172	118	199	0	15	504
Sum	0	4,803	4,896	-------	-------	-------	22,925
Minus 1934	0	4,432	4,647	7,447	-------	-------	22,000
Minus 1924 and 1934	0	4,316	4,467	7,308	4,779	248	21,118
Percent	-------	20.44	21.15	34.61	22.63	1.17	100.00

TABLE 26.—*The total escapement of Karluk River sockeye, 1921 to 1950*

Year	The escapement by periods in thousands*							
	to May 31	June 1 to June 21	June 22 to July 19	July 20 to Aug. 16	Aug. 17 to to Sept. 13	Sept. 14 to end of season	Aug. 17 to end of season	Total
21	22	488	195	341	280	174	454	1, 500
22	10	95	98	41	77	79	156	400
23	73	134	80	153	171	84	255	695
24	91	341	134	210	?	?	287	1, 063
25	63	494	125	291	409	239	648	1, 621
26	561	610	149	365	723	125	848	2, 534
27	62	483	76	92	77	83	160	872
28	166	477	134	129	125	63	188	1, 094
29	76	253	34	142	309	87	396	901
30	44	286	46	287	251	183	434	1, 087
31	63	183	43	149	318	117	435	873
32	49	273	50	58	131	177	308	738
33	27	354	138	112	292	64	356	987
34	204	522	39	?	?	?	?	1, 450
35	162	268	11	119	184	132	316	876
36	183	255	84	82	676	96	772	1, 375
37	5	787	86	71	222	94	316	1, 265
38	0	732	95	42	?	?	361	1, 230
39	84	246	48	75	207	46	253	706
40	269	290	42	28	?	?	187	816
41	226	137	53	136	?	?	380	932
42	153	155	45	68	144	64	208	629
43	155	394	75	56	?	?	241	921
44	99	236	19	73	?	?	342	769
45	60	353	51	107	75	13	88	659
46	65	211	40	9	39	78	117	442
47	5	189	46	121	117	7	124	485
48	179	345	43	94	85	8	93	754
49	34	307	48	134	162	6	168	691
50	48	288	52	68	270	33	303	759
um	3, 238	10, 186	2, 179					29, 135
Minus 1934	3, 034	9, 664	2, 140	3, 653			9, 194	27, 685
Minus 1924 and 1934	2, 943	9, 323	2, 006	3, 443			8, 907	26, 622

*Adjusted to date of catches at mouth of Karluk River to discount time spent in upstream migration to the counting weir.

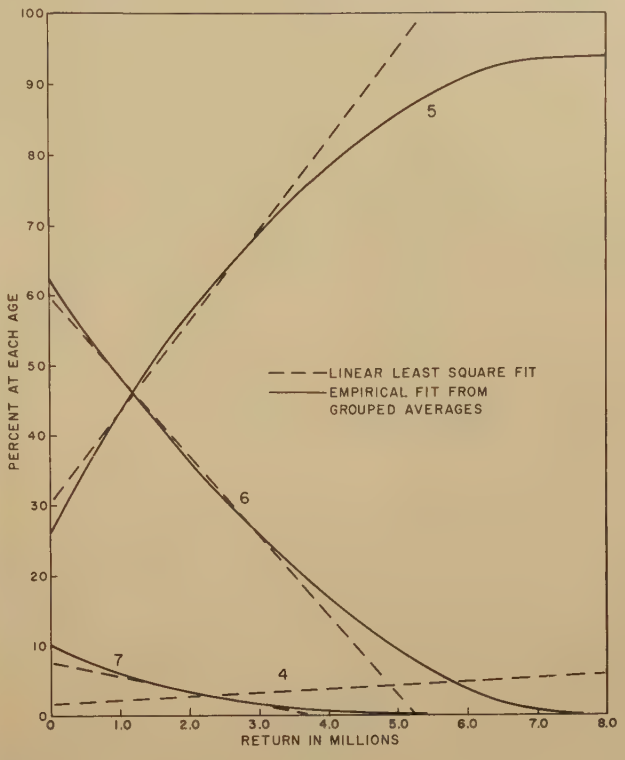

FIGURE 50.—Showing the linear least square and the empirical fit from grouped averages to the percent of fish returning at each age on the size of the brood of which they are a part.

Table 28 and figures 52 and 53 show the runs and escapements by spring, summer, and fall periods. It will be noted in figure 52 that the three seasons show the same general pattern of decline. The 1931–35 period is low as 1934 data on seasons are incomplete, necessitating omission of that year. The escapements (fig. 53) for the spring and fall seasons are obviously a function of the size of the runs. As the 1921–25 escapements are largely the source of the 1926–30 runs, and so forth, it is also clear that the relative size of the spring and fall escapements bears no relation to the relative size of the ensuing seasonal runs.

The summer escapement fell off rapidly and remained very low, yet the summer runs followed the same pattern as the other runs. It is almost necessary to conclude that the three seasons followed the same general pattern and did not respond to changes in the escapement for the respective seasons.

Thompson (1950) attempted to show that the decline in the Karluk runs was caused by a decline in the summer runs, accompanied by a relative increase in the spring and fall runs. This is similar to the drop in the summer sockeye run to the Fraser (Rounsefell and Kelez, 1938, p. 764). However, the drop in the Fraser run could be attributed to a decline in the races of sockeye that migrated through the fishery at a particular season. This is not the same at Karluk.

The data presented by Thompson on Karluk seasonal case-pack (taken from his mimeographed figures) for the 25 years from 1895 to 1919 for one cannery are compared in figure 54 with the seasonal catch at Karluk for 28 of the 30 years for which data are on hand from 1921–50. These curves refute the proposition that the seasonal catch bears any close relation to the seasonal run (compare figs. 33 and 54), or that the data he presents can be interpreted as showing any relative decrease in the summer run.

The slightly lesser importance of the fall catch in the later years can well be due to the early closing of the fishing season in many of the late years. All evidence appears to point to one pop-

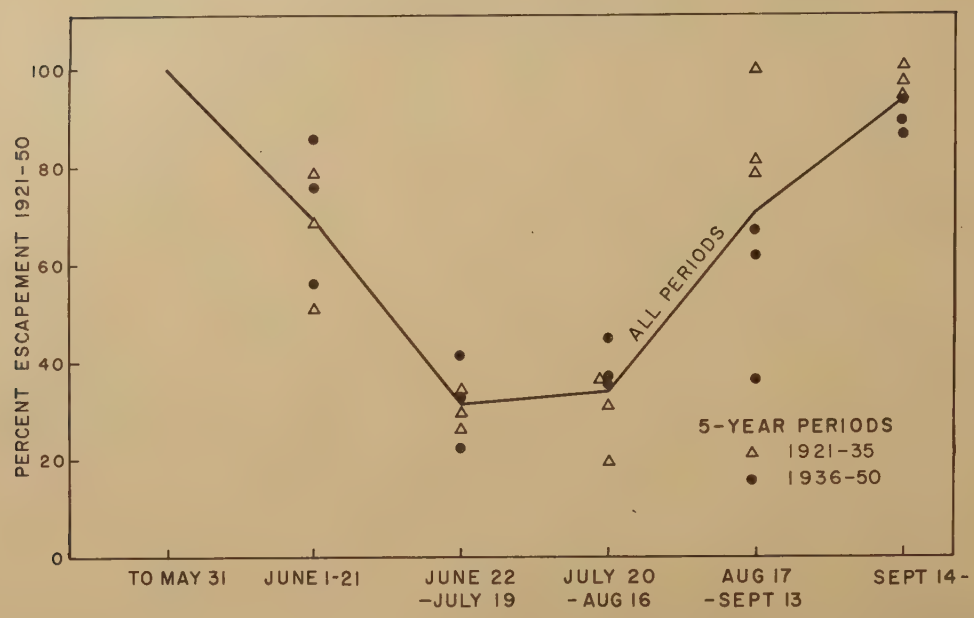

FIGURE 51.—Percentage of the run escaping through the fishery, by 4-week periods, from 1921–50.

TABLE 27.—*Percentage of total run escaping by periods, 1921 to 1950*

Year	to May 31	June 1 to June 21	June 22 to July 19	July 20 to Aug. 16	Aug. 17 to Sept. 13	Sept. 14 to end of season	Aug. 17 to end of season
1921	100.0	93.3	33.1	36.6	33.1	75.7	42.2
1922	100.0	70.4	49.0	19.0	19.5	77.5	31.4
1923	100.0	48.7	38.8	37.6	46.2	89.4	55.0
1924	100.0	74.6	42.7	60.2			38.7
1925	100.0	92.2	45.3	30.5	46.7	100.0	67.1
1926	100.0	72.2	32.0	32.1	40.2	91.2	44.4
1927	100.0	93.4	29.7	22.9	28.7	100.0	45.7
1928	100.0	81.3	40.0	21.6	39.1	70.8	46.0
1929	100.0	81.6	29.1	62.0	100.0	100.0	100.0
1930	100.0	99.7	30.9	85.2	99.2	99.5	99.3
1931	100.0	63.3	22.6	44.1	56.7	63.6	58.4
1932	100.0	63.2	24.2	21.2	47.8	100.0	68.3
1933	100.0	46.8	46.6	36.7	81.8	90.1	83.2
1934	100.0	58.5	13.5				
1935	100.0	48.9	6.5	40.5	81.1	100.0	88.0
1936	100.0	42.3	29.7	13.4	100.0	100.0	100.0
1937	100.0	72.4	24.9	23.8	43.8	100.0	52.6
1938		78.0	33.3	10.6		100.0	60.7
1939	100.0	54.1	21.1	40.2	99.0	90.2	97.3
1940	100.0	95.7	40.4	12.2			51.5
1941	100.0	47.4	52.0	37.1			58.9
1942	100.0	53.6	29.8	34.9	50.7	100.0	59.8
1943	100.0	58.4	25.9	34.4		100.0	54.3
1944	100.0	46.9	11.0	24.8	100.0	100.0	100.0
1945	100.0	50.3	20.1	49.3	84.3	100.0	86.3
1946	100.0	85.1	29.4	8.7	100.0	100.0	100.0
1947	100.0	86.3	66.7	68.8	98.3	100.0	98.4
1948	100.0	76.8	16.2	22.2	98.8	100.0	98.9
1949	100.0	80.8	29.6	33.8	100.0	100.0	100.0
1950	100.0	62.6	30.6	25.5	100.0	68.8	95.3
1921–25	100.0	75.8	41.7	36.8	36.4	85.8	46.9
1926–30	100.0	85.6	32.3	44.8	61.4	92.3	67.1
1931–35	100.0	56.1	22.7	35.6	66.8	88.4	74.5
1936–40	100.0	68.5	29.9	20.0	80.9	97.6	72.4
1941–45	100.0	51.3	27.8	36.1	78.3	100.0	71.9
1946–50	100.0	78.3	34.5	31.8	99.4	93.8	98.5
1921–50 [1]	100.0	69.3	31.5	34.2	70.5	93.0	71.6

[1] Average of 5-year periods.

ulation of sockeye at Karluk, the adults returning at various ages and seasons, the age and season depending to a large extent on varying ecological conditions.

DISCUSSION

Before formulating an hypothesis to explain the facts brought out by the foregoing analyses it may be worthwhile to discuss briefly the explanations for the general decline made by various persons at various times. These will be discussed one at a time, the list includes the following:

a. Long-term changes in the physical environment.
b. Increased predation on young sockeye.
c. Overfishing on one (or more) of several discrete populations in the Karluk runs.
d. Overfishing in general.
e. Reduction in lake fertility.

Long-term changes in the physical environment

The data on temperature and rainfall shown, exhibit fluctuations covering periods of several years. Nevertheless, over the whole period of years of available data (table 5 and fig. 9) there is no general change either in temperature or rainfall. Therefore, although they are the cause of some of the short-term fluctuations the available evidence indicates that those two physical factors cannot be the cause of the general decline.

Increased predation on young sockeye

This theory for the decline was never fully advocated by biologists but rather by some of those entrusted with the management and enforcement of the fishing regulations, and many persons in the fishing industry. Unfortunately, the whole theory fell into disrepute on two grounds. (1) No

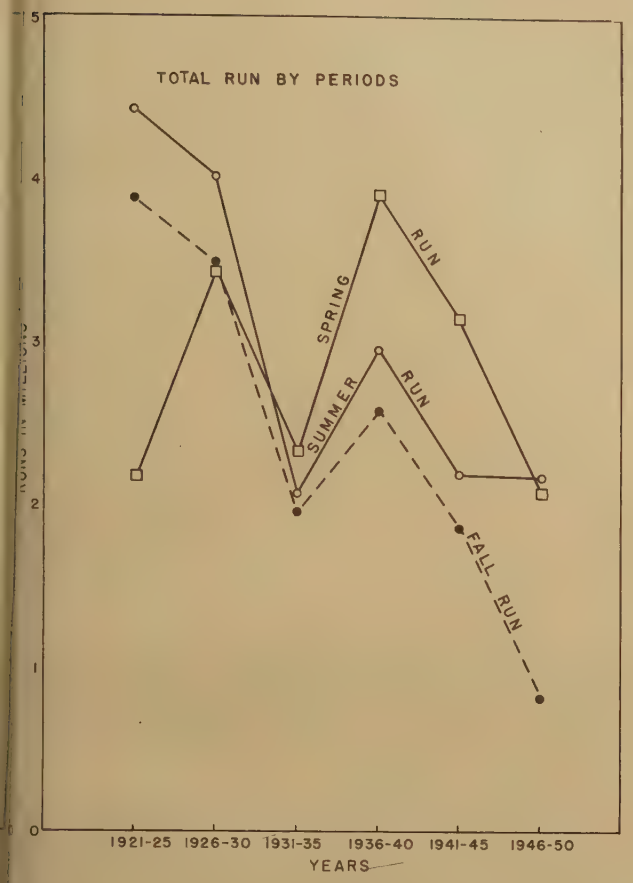

FIGURE 52.—Comparison by 5-year periods of the spring, summer, and fall runs.

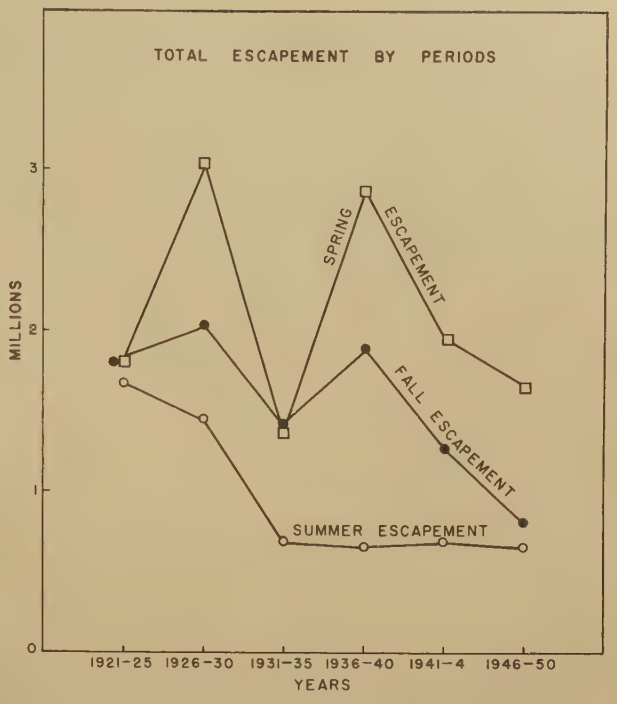

FIGURE 53.—Comparison by 5-year periods of the spring, summer, and fall escapements.

adequate tests, such as were made at Cultus Lake, were carried out in Alaska so that no accurate measure of the effect of destroying predators was obtained. (2) The destruction of predators was carried out over a wide area in Alaska, chiefly on the basis of bounties to native fishermen (Hubbs 1940), and financed by the Territory and by the canners. Naturally, bounty seekers fished for predators only where they were most abundant and most easily captured.

Capture of only a portion of a predator population at the time when it is at a peak may result in increased future predation. Let us postulate a population of a million predators, which in the course of events will soon be reduced to 300,000

TABLE 28.—*Runs and escapements by 5-year periods, 1921–50 (in thousands)*

Period of years	Total run by periods			Total escapement by periods			Total run	Total escapement	Average total run per period	Average total escapement per period
	to June 21	June 21 to Aug. 16	Aug. 17 to end of season	to June 21	June 21 to Aug. 16	Aug. 17 to end of season				
1921–25	2,185	4,443	3,895	1,811	1,668	1,800	10,523	5,279	3,508	1,760
1926–30	3,455	4,027	3,502	3,018	1,454	2,026	10,984	6,498	3,661	2,166
1931–35*	2,327	2,071	1,983	1,379	680	1,415	**6,381	**3,474	2,127	1,158
1936–40	3,927	2,969	2,590	2,851	654	1,889	9,486	5,394	3,162	1,798
1941–45	3,151	2,206	1,880	1,968	683	1,259	7,237	3,910	2,412	1,303
1946–50	2,087	2,170	823	1,671	655	805	5,080	3,131	1,693	1,044
Grand total	17,132	17,886	14,673	12,698	5,794	9,194	49,691	27,686		
Minus 1921–25	14,947	13,443	10,778				39,168			
Minus 1946–50				11,027	5,139	8,389		24,555		
Escapement as percent of runs during the ensuing 5-year periods				73.77	38.23	77.83		62.69		

*Minus 1934.
**Includes 1934.

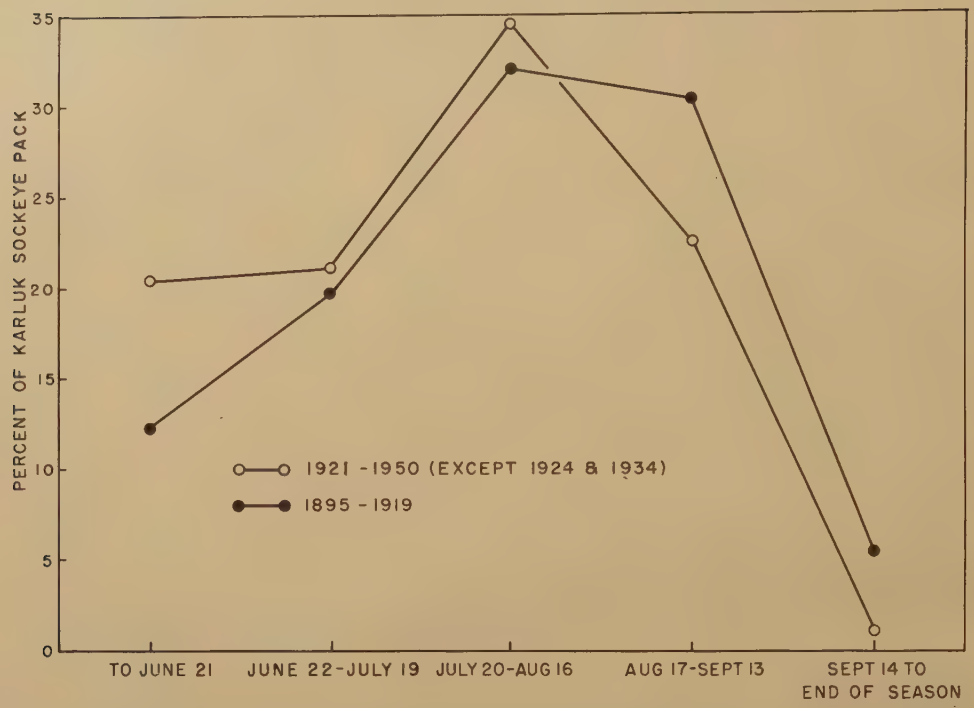

FIGURE 54.—Percent of the sockeye pack canned during different portions of the season for the 1895–1919 period compared to the 1921–50 period.

through natural control (in this instance, lack of sufficient young sockeye for food). If we now capture 400,000 of this predator population the remaining 600,000 will have more food per predator and survival will likely exceed the 300,000 which would have survived without any attempted control. Thus, a smaller predator population will thrive better than a larger in seasons when the number of young salmon prey are too small to support the greater number of predators.

At Karluk the destruction of predators was confined to attempting to destroy large numbers of Dolly Varden charrs by seining or trapping at the salmon-counting weir during their annual downstream migration in May and June. In the 21 years from 1922 to 1942 the annual reports of the Alaska Division mention the destruction of Dolly Vardens during 15 years. During the 9 years in which the numbers destroyed are recorded they vary from 3,000 to 81,500. The work was hampered by high water and by the desire to avoid harming the downstream sockeye migrants. These migrants commence their seaward migration soon after that of the Dolly Vardens and there is considerable overlap.

DeLacy and Morton (1943) have shown that many Dolly Vardens are found in the tributaries of Karluk Lake during the season when those that have migrated downstream are at sea, so it is obvious that not all the Dolly Vardens were subject to capture at the weir.

Since DeLacy and Morton (1943) also found large numbers of nonmigratory alpine charr (*S. alpinus*) in Karluk Lake, the utility of the destruction of Dolly Vardens alone is questionable. Certainly it does not constitute any test of the results that might accrue from a full-scale program of predator control.

Overfishing of one (or more) of several discrete populations in the Karluk runs

This theory depends of course on the existence of discrete populations. One advocate of this theory is Thompson (1950) whose hypothesis of summer overfishing of a discrete population is based on a comparison between the salmon pack of earlier years and the weir counts of salmon bound for the spawning grounds in later years. As figure 54 shows, one can not compare pack during one period with escapement in another period as escapement was not uniform in different parts of the season.

The existence of a midsummer lull in the runs l many to postulate the existence of "spring" d "fall" runs of salmon belonging to self- rpetuating populations. This theory has long en generally accepted without any proof. For any years the attempt to assure a spawning ock for the spring and fall runs has doubtless ntributed to the condition whereby the smallest lative escapement has been coming from the lmon running in the center portion of the season. is is unfortunate since the eggs and young of ese fish are more apt to encounter favorable mperature conditions.

As abundant proof has been offered to show that ly one population exists this topic need not be pursued further.

verfishing in general

This theory for the decline at Karluk once emed thoroughly reasonable. It was based on e idea that the existence of the 5-year cycles in e run (during the earlier years) is adequate oof that the returns are in direct proportion to e escapement since the majority of the run are sually 5 years of age. As we have shown, the turns are not directly proportional to the escape- ent. The reproduction curve shows a decreas- g survival rate with an increasing number of awners. It has also been shown that the cycles ersisted despite this type of reproduction curve ecause of the relation between the survival of oung fry and the lake density of older young, hereby the large numbers of young from the rger broods exerted an unfavorable influence on e young of the smaller broods and vice versa.

Good escapements of spawning fish were ob- ined in every year following the enactment of e White Act of 1924. However, instead of llowing the principle of allowing 50 percent of e run to escape, an attempt was made through osure of fishing to obtain a larger proportionate scapement in the low years by requiring a mini- um of a million spawners. As we have shown, is did not halt the decline in the runs (it may ave accelerated it) because it soon destroyed the alanced cycles, that had endured for many years, hich favored the survival of the large broods and ilitated against the small broods. This increase f the escapements in the low years quickly amped the former regular oscillations in the umbers of young sockeye in the lake. This rend toward stabilization of the annual numbers of young produced removed the natural control of density-dependent predators which were no longer held in check by alternate feasts and famines.

The belief that the decline in the runs was caused by overfishing was abandoned as untenable after increased runs did not result when ample spawning fish were reserved over a period of years. It is not the rate of exploitation that has changed, but the ability of the populations to withstand even a greatly diminished rate.

Reduction in lake fertility

After all other explanations for the general decline in abundance failed the most popular explanation has been a supposed progressive decline in fertility of the waters of Karluk Lake. The only evidence to which advocate of this proposition can point is the long-term decline in abundance of the runs combined with the failure to discover any alternative explanation. The fact that there has been a tendency for the average age at maturity to increase has also been cited in support of this theory. The increase in average age is confirmed but it is also found that the age composition of each brood varies with the size of the brood, the largest broods having a younger average age. The increase in average age can therefore be explained wholly on the basis of the smaller returns, since (see appendix J) small broods of young tend to remain longer in the lake because their small biomass raises the individual threshhold size necessary for seaward migration.

If the increase in age at return were due to increased intra-specific competition from lowered lake fertility, then smaller broods should tax the food supply less, grow faster, and show a lower average age. The reverse is true.

The hypothesis that the decline in the runs has come about through a gradual decline in lake fertility is based on theoretical grounds. It is known that the carcasses of the dead spawners contribute a large quantity of chemicals, of which nitrogen and phosphorus are important, to the lake waters; also that these chemicals are used to produce food organisms consumed either directly or secondhand by young sockeye.

The truth of the theorem depends on the truth of three major premises, to wit: (1) That the decomposing carcasses furnish a very large share of the nutrients available to the primary food organisms, (2) That there has been a large but gradual

decline in the number of spawners and, (3) That the fertility of the lake has actually fallen to a significant degree.

Those who accept the three major premises appear to be divided into two schools of thought concerning the manner in which the runs are presumed to be affected. One school holds that the fertility of the lake in any period depends to a large extent on the gradual release, over a long period of years, of chemicals stored from the carcasses of adults that spawned in the lake many years before. They reason that since there has been a decline in the number of spawners, this storehouse is gradually becoming exhausted.

The other group contends that because of a continuous decline in the number of spawners the nutrients available each year from decomposing carcasses are becoming increasingly insufficient.

The storage and gradual release theory requires proof since practically all work on fertilization of waters has been carried out in farm ponds and small shallow lakes in which the volume of water is extremely small in relation to the area of bottom deposits. Karluk Lake (Juday et al., 1932) has a maximum depth of 126 meters (413 feet) and a mean depth of 48.6 meters (159 feet).

The constant loss of chemicals through lake outflow also makes it appear unlikely that any long-term decline in fertility could be caused by any using up of chemicals stored in the lake itself over long periods. Between 1926 and 1940 (tables 26 and A–11) the 3- and 4-year smolts leaving the lake weighed 194 metric tons per year, or about 200 metric tons if we allow for the few 2- and 5-year smolts. The average escapement of sockeye into the lake was 1,120,000 fish. Allowing 2 kilos per fish this yields 3,360 metric tons of adults so that the ratio of income to outgo stands at about 17 to 1. If we assume ocean mortality to have been relatively constant over the years this ratio should have been about the same during the earlier years.

Concerning the relative quantities of terrigenous phosphorus and that contributed by the salmon carcasses, Nelson and Edmondson (1955) state,

> . . . measurements were made of the phosphate at the mouths of tributary streams in the period when the salmon were decomposing in the streams, and on the same streams the phosphate content was determined above the salmon spawning areas, or at the stream outlets prior to the entrance of the fish. Results from this work show almost a fourfold increase (from 0.008 milligram/liter to 0.029 mgm./l.) in phosphate in the stream water during the spawning period of 2 to 3 months.

Although published data on the chemistry of the streams tributary to Karluk Lake are too scanty to make any formal prognosis, those available seem to show that the importance of the salmon carcasses as the source of nutrient materials may have been overemphasized in the past. In table A–15, appendix K, is shown the soluble phosphorus for tributary streams of Karluk Lake from published data.

We believe these data indicate that there is a natural increase in soluble phosphorus between the upper and lower reaches of these streams and that the above-mentioned figures of 0.008 and 0.029 mgm./l. do not take this into account. The water in the upper portion of a stream will contain less soluble phosphorus but Nelson and Edmondson apparently averaged these upstream values in with the values taken at the mouth before the salmon arrived, to obtain the figure of 0.008. Using only observations from the same areas of the streams (table A–15) the data suggest that the annual terrigenous contribution of soluble phosphorus exceeds the extra supply during the 2- to 3-month period when the salmon carcasses are decomposing.

Using the more reliable estimates of total phosphorus it is also suggested (appendix K) that the terrigenous contribution of total phosphorus is larger than the total phosphorus from most annual escapements.

As to the second theory, reduction of escapement, the present analysis of the runs show from the reproduction curve that the largest total runs come from moderate numbers of spawners, so that in prefishing years (see 0 fishing rate on upper curve in fig. 21) the runs very likely averaged only slightly more than 2 million fish. If adequate data should confirm the suggestion that the terrigenous phosphorus annually entering the lake is equivalent to nearly twice the amount contained in the carcasses of 1 million adult sockeye, then the reduction in the total phosphorus content of the lake caused by reduced escapements is in the order of 10 to 15 percent over a period of about 75 years.

Intraspecific competition for food (within the range of 4 to 13 million smolts) would seem to be ruled out as a limiting factor not only by the highly significant linear relationship between

nber of smolts and their total weight, but by actual increase in individual weight in the ger broods. Thus, if we correlate the number smolts migrating (column 5, table A–11) with weight of the individual 3-year-old smolt in migration of the same year (column 4, table 10) the coefficient of correlation is 0.5936 and nificant. This strongly indicates that survival the smolt stage is partially a positive function rate of growth. This does not mean that the nsity of food organisms is not important. The erpretation suggested is that when the density food organisms is high two results occur: survival is enhanced by the increased growth e, resulting in a large brood, and the size of the ividual fish tends to be large.

Were the annual survival of young dependent available food at some short critical period re would be no logical reason to expect any ect on the relative size of the survivors of ferent broods. Therefore, the chief cause of s relationship can be assumed to be heavier ses through predation on the slower-growing oods. This does not answer the question as whether there has been any long-term decline fertility of the lake, since a lower level of preda- n (in the absence of intraspecific food competi- n) undoubtedly would raise the rate of survival.

To sum up the foregoing the general decline rate of survival can stem principally from three ises:

1. Increased predation on the young through k of control of the density-dependent predators. is may have come about through a decrease the amplitude of the oscillations, formerly so nounced, in the number of spawners.

2. Higher mortality of young caused by in- ased loss to predators during a longer sojourn the lake before making the seaward migration. is longer sojourn appears to be due principally an insufficiently large total weight of young in st years to induce early migration.

3. Heavier losses from predation in the lake used by a slower rate of growth. Since there good evidence against the existence of any nificant intraspecific competition for food in cent years, the smaller average individual smolt e of the less numerous broods may indicate a wer growth rate in recent years, possibly used by a drop in lake fertility. With a slower te of growth more of the slow-growing broods would be taken by the same number of predators. However, the same differential mortality between broods may have been occurring in former years but have become more pronounced with more predators so that the data cannot confirm but certainly cannot deny a drop in lake fertility.

The foregoing analysis of lake fertility (see appendix K) is based of course on the assumption that there has been no significant change over the period of the fishery in the annual contribution of terrigenous phosphorus (or other nutrients). It does not, however, take into account the possibility that there may have been a gradual long-term decline in the chemicals leaching into the lake from the watershed. The soils in the general area of southwestern Alaska have been enriched from time to time by deposits of volcanic ash. The marked effect on fertility in certain lakes following the Katmai eruption of 1912, and the subsequent enrichment of the soils, is described by Eicher and Rounsefell (1957). The Karluk watershed was just south of the area of ash deposit from Katmai (10 inches fell at Kodiak) but probably it has received ash deposits in the more distant past.

The destruction of the former cycles of big and small years that prevailed over several decades may have had a much greater effect than we can ascertain. The portion of the effect that we have removed statistically is only that portion that is caused by intraspecific competition between broods (probably including some degree of cannibalism). The general decline that could have been caused by multiplication of species density-dependent upon sockeye (predation and competition could both be involved) because of the cessation of control over these other species when the cycles were destroyed, cannot be estimated from these data.

In regard to the second point it has been shown that there appears to be a threshhold size which a young fish must attain in order to become a smolt and migrate seaward, and that, further, this threshhold size is a variable that changes inversely as the weight of the biomass of smolts in the migration.

Concerning the effect of biomass of young in inducing migration from Cultus Lake, Foerster and Ricker (1948, p. 204) state,

> The yearling stock is thus 28 percent of the lake's total g in of sockeye biomass in years before (predator) control,

and 44 percent of it after control, on the average. The apparent improvement in utilization of production is therefore about 55 percent. However, yearling stock is not exactly the same thing as yield, and in some of the years before control a large part of it did not migrate.

It is not possible from the data to know which of these three points is paramount but all may have been instrumental in causing the general decline. Because we have no good measure of the mortality in the lake of young that remain an additional year before migrating, it is not possible to assign one portion of the decline to heightened mortality of young up to their third year and another portion to the additional mortality on the proportion of the young that remain an additional year on account of lack of a sufficiently high biomass of smolts to induce migration.

We have no positive evidence to support the theory of declining fertility, but let us suppose that it might be feasible to increase fertility through artificial fertilization of the waters. Would this result in a greater survival of young sockeye? It might at first, however, if the fertilization were continued the predators would merely need to increase to lower the survival rate to the point where most of the advantage of the increased growth from the larger quantity of available food was being lost by heightened mortality, so that the end result might be no increase in the weight of the smolt biomass migrating from the lake unless predator control were conducted simultaneously. The experiments of Nelson and Edmondson (1955) show that sockeye growth was increased by fertilization of Bare Lake, a 120-acre unstratified lake lying near Karluk in the Red River watershed. Experiments on larger stratified lakes are now needed to determine the feasibility of fertilization of lakes similar to Karluk.

Control of predators density-dependent upon sockeye may be accomplished by varying the food supply of these predators through great variations in the abundance level of young sockeye from year to year. In order to take full advantage of such control it may even be necessary to re-establish the former cycles. This natural control having been destroyed it may be very difficult to restore the runs unless these other fishes are controlled by man.

A somewhat similar situation is recorded by Smith (1955) for brook trout in Crecy and Gibson Lakes, New Brunswick. He concludes,

Stocking alone was found to be ineffective in Cre other lakes of the area (Smith 1952a). Stocking of Lake, when a barrier was present in the outlet to p escapement of planted trout, was also ineffective. zation and stocking when applied together led to im ment of the yield of trout from Crecy Lake, but, as w seen, only temporarily until predator control was taken.

It has been shown for Cultus Lake (Roun 1946, see fig. 3) that control of other fishes gr increased the total poundage of seaward migr This increased biomass of migrants was obta without an increase in actual productivity o lake. This follows because under condition heavy predation a large portion of the food sumed by young sockeye does not contribut the final biomass. Predator control at Cu Lake accomplished two things: (1) it raised survival rate so that fewer spawners could sup all the young required (2) it raised the conver rate of natural food into sockeye migrant flesh that more or larger smolts could result from same lake area.

It appears from the preceding that the differe in survival rate between early and recent ye stems from two causes: higher mortality in rec years from the time of egg deposition to the th year, and in recent years a higher mortality fish after their third year because more of th remain an additional year in fresh water.

The remedy for both lies in increasing the b mass of smolts. To increase the number spawners without regard to sources of mortal might help by increasing egg deposition to a po where the number of smolts produced was la despite heavy mortality in the lake, perhaps la enough to gain the additional benefits of ear smolt migration.

This method appears to be highly wasteful. the same results can be achieved without increased number of spawners the econo benefits will be large indeed. We, therefo recommend trying certain logical steps, includ control of predation on adults and young, provement of spawning grounds, some shift in seasonal proportion of the run reserved for spa ing, and experiments to determine the feasibil of increasing growth rate by fertilization of la stratified lakes.

The collection of sufficient field data to de mine the role of each predator or competitor be so involved and time consuming that a di

proach is indicated. This would involve ex-ding from the lake all potential anadromous edators, coho and king salmon, charrs, and outs, and in the lake itself in netting or trapping remove all possible charrs.

The effect of controlling the fresh-water sculpin uld be measured by experiments on paired eams. Shapovalov and Taft (1954, p. 251–256) ow that two species of sculpin, *Cottus asper* and aller *Cottus aleuticus* can be controlled in lifornia streams by low barrier dams. The ulpins make a definite annual downstream mi-ation. On returning, the sculpins are unable pass the low dam used for an experimental fish ap, and so they were soon heavily depleted above e dam. From 3,357 sculpins moving down-eam the first year, the run fell to 337 in 3 years d to 30 sculpins in 8 years. In neighboring ott Creek no sculpins now live above a low dam ilt in 1908, although they are still abundant low it.

Since *Cottus aleuticus* Gilbert is also the fresh-ter sculpin present in the Karluk River system vermann and Goldsborough, 1907) a trial of is method of control is clearly indicated.

That the Karluk River sculpins probably also rform definite migrations is perhaps indicated the experience of Cloudsley Rutter (Chamber-n 1907). During the night of June 25, 1903, a ke net with a 25-foot wing spread set at the tlet of Karluk Lake in the river took 738 ulpins.

Since the desired objective is to produce the rgest surplus of returns over number of spawners, e suggest strict control of predation on the awning salmon, by bears.

A study needs to be made jointly by biologists d engineers to determine the costs of making ysical improvements in the limited spawning ea available in the streams. These might in-ude the placing of large boulders to stabilize ifting gravel bars, establishing very low dams spawning areas to keep the beds from becoming posed in dry weather, or freezing deeply in nter, making additional space for spawning by moval of excess boulders, and construction of od control headwater dams with controlled tlets to provide stabilized stream flows.

Concerning the relation between the time of n and the time of actual spawning, Gilbert and ich (1927, p. 27) state,

> The first fish to appear are, in general, well advanced toward spawning and certainly do not linger long in the lake before seeking the spawning gravels. The earliest spawning has not been observed, but it is believed to take place not later than the middle of June. From that time until late in the fall uninterrupted spawning is in progress in suitable gravels about the shores of the lake and in all favorable tributaries.

On the average, neither the very early nor the very late spawners are as successful as those spawning in midseason. The analyses showed that because of the deleterious effects on survival of low autumn (11 out of 48 years) and late spring (about 14 out of 47 years) temperatures, survival depends to some extent on the season of spawning. It would be best then to abandon the idea of obtaining a spring and fall group of spawners, but rather to encourage the canning of the early and late fish, and insist on a higher percentage of the summer fish being in the escapement. This should, on the average, raise the survival per spawner, which would increase the runs during all parts of the season.

The Bare Lake experiments (Nelson and Edmondson, 1955) have shown that the growth rate of young sockeye can be increased by fertilization in a small unstratified lake. The feasibility, both biologically and economically of fertilization of Karluk Lake should be determined by experiments on a lake larger and much deeper than Bare Lake.

SUMMARY

After the inception of canning in 1882 the Karluk River sockeye catches rose quickly to a maximum and then declined gradually over several decades. Catch records are available since 1882 plus actual weir counts of the upstream-migrating salmon since 1921. Ages of salmon in the runs by weeks are available for 1922 and continuously since 1924.

Runs in the neighboring streams show the same secular changes in abundance (after removal of the short-term 5-year cycle) as the Karluk runs, indicating a common cause. The changes in survival at Karluk are significantly correlated with variations in temperature. Autumn temperatures averaging below 34° F. lower survival from the eggs then in the spawning gravels. April and May temperatures affect the survival of the brood resulting from eggs deposited the previous season, the effect probably being greatest

on eggs deposited the previous late spring. Either too low or too high a temperature lowers survival; the optimum survival range lies between 39° and 42° F. The accumulated monthly temperature between 45° and 55° F. for the two years succeeding egg deposition affect survival of young, presumably by affecting growth. The optimum survival occurs between an accumulation of 45° to 60° F. Greater or lesser accumulation lowers survival.

Rainfall for the period April to July in the year following deposition of the eggs affects survival of a brood, presumably through the effect of drought or floods on the fry emerging from the gravel. For this period survival declines sharply as the total rainfall falls below 14 inches. Above about 20 inches of rain the survival only decreases gradually, probably owing to freshets.

Survival of sockeye from broods of odd-numbered years is very significantly and consistently higher than from broods of even-numbered years. The even-numbered years are those of the cycle of pink salmon that has remained dominant at Karluk at least as far back as 1880.

The survival from any brood is negatively correlated with the numbers of young sockeye two and three years older in the lake during the season the brood emerge as fry. This 2½-year negative correlation between fry survival and lake density of older young results in a positive 5-year cycle in the runs, which has previously been erroneously ascribed to the effect of age.

After statistical removal of the variation caused by these physical and biological factors it is clear that the sockeye has a dome-shaped reproduction curve. This indicates that, on the average, the largest available surplus of returning adults over the number of spawners occurs with intermediate numbers of spawners.

The general decline in the sockeye population can not be ascribed to the above factors since they exhibit short-term, not long-term fluctuations. Neither is the decline caused by the number of spawners, which has been fairly high in recent years. The decline is caused by a lowered survival rate in recent years.

Analysis of the age composition of both the seaward-migrating smolts and the returning adults shows that the particular portions of the season at which adult sockeye return to the river (extending from May to October) is governed by two equally strong and opposing factors: smolt age and ocean age. Smolts leave the lake in the late spring and early summer of various years of life. These years in the usual order of importance are 3, 4, 2, and 5. Some young enter the sea in their first year but so few sea-type adults return and the mortality is doubtless so high that the relative number is unknown. With the exception of these few sea-type fish, those leaving at the younger ages tend to return earlier in the season during their spawning run. However, those remaining the shortest time in the sea (they remain from less than 1 summer to 4 summers at sea) tend to return later in the season.

It is shown conclusively that the modes of abundance in the curve of total annual runs to the river are caused by the different times at which these different age combinations of smolt- and ocean-age fish return and not, as previously supposed, to any racial differences. This lack of races is further borne out by significant correlations between fish of the same brood that return at different ages in different portions of the season.

A tendency for an increase in the average age of the returning sockeye in more recent years has been ascribed previously to loss of lake fertility. This increase in average age is confirmed, but it is also shown that the average age of return of each brood is correlated with the size of the brood. Larger returns contain more younger fish. This increase in average age thus may be merely the result, without necessarily any causal relation, of the dwindling runs in recent years.

It is shown that the relation between numbers and biomass of the annual Karluk smolt migration is strictly linear, indicating no intraspecific competition for food within the range of smolt populations available in the data (4,675,000 to 13,226,000). At Cultus Lake the smolt biomass shows a linear relation to the logarithm of the number of smolts, indicating that the food supply is being heavily taxed by the larger populations. Karluk Lake produces more than four times the weight of smolts per acre as Cultus Lake. This is probably caused by the difference in surface water temperatures which in Karluk Lake are optimum for young sockeye growth but in Cultus Lake are so warm that the young are confined for 3 months to the stratum adjacent to the thermocline. This shows that the continual decline in the Karluk

ns is not caused by intraspecific competition for e available food.

The attempt to stabilize the runs by obtaining high number of spawners in every year has rgely destroyed and obscured the former cyclic aracter of the runs. During the period when ese cycles were present the number of spawners ctuated in a more or less regular manner from ry high to very low (lower than most recent ars). This wide variation in number of spawners sulted in wide oscillations in the numbers of ung sockeye present in the lake and therefore ailable as food for predator fishes. These gular oscillations in the supply of available prey y have acted as a control on the abundance of edators.

Apart from knowledge of the tremendous abundce of fish predators at Karluk, young of coho and g salmon, Dolly Varden charrs, alpine charrs, elhead rainbow, and freshwater sculpins, there scant quantitative data on them, but their great portance is clearly indicated.

RECOMMENDATIONS FOR ACTION

This report is an attempt to postulate reasonable potheses to explain the observed facts. In some stances the data are sufficient to afford definite oof, but in others they can only furnish strong dications. Therefore, in evaluating the final ommendations it must be borne in mind that ly further careful research can fully prove, or for at matter disprove, the validity of some of the potheses upon which they must rest.

Furthermore, where more than one factor is dicated as operating to bring about some contion, the data are not always sufficient to yield y good estimate of which factor is the more imrtant. Bearing these limitations in mind, but so realizing the necessity for action to arrest the clining abundance, conclusions have been reached at, although they later may be modified, give a sis for action consonant with the present state our knowledge.

It is concluded that the survival rate can be creased in six ways listed more or less in the order their importance: (1) by eliminating so far as racticable all predator species of fish from Karluk ake and its tributaries, (2) by regulating the fishg in such a manner that greater numbers of awners are from the middle portion of the runs nd smaller numbers from the early and late portions of the runs, since the spawning success of the latter is often adversely affected by autumn and spring temperature conditions, (3) by restoring insofar as practicable the former cyclic character of the runs in order to lessen competition between the older young and fry, and perhaps give some measure of natural control of predators. Because of the present low state of the runs this should be accomplished by providing a higher proportion of spawners on big runs rather than by decreasing the proportion on smaller runs, (4) by increasing growth rates through fertilization of the lake waters (if it is proved to be economically feasible), (5) by physical improvement of the spawning beds, (6) by increasing the egg deposition of the potential spawners through control of predators on the adult run.

Recommendations 2, 5, and 6 are all designed to obtain the largest possible number of fry per potential spawner. This is doubly important with the present small runs.

Recommendation 1 is of great importance at present. If, after restoration of larger runs, it is found that either through natural predator control (see recommendation 3), or through accelerated early growth (see recommendation 4), the artificial control of predators is no longer necessary, it may be possible to discontinue it. Both 1 and 4 are designed to increase the biomass of young by lowering predation. One will also increase the biomass, even without increasing available food supplies, by conserving food otherwise lost by predation after consumption. Four may be necessary to supplement 1, at least at first, since the biomass of the present small broods, even with predator control, may not sufficiently lower the threshold size at seaward migration to induce seaward migration at an early age without faster growth.

Recommendation 3 might not have to be carried out if predators are strictly controlled, but this is uncertain because the data available do not give sufficiently clear indications of the relative importance of predators and intraspecific competition (possibly cannibalism). This is a point on which research is sorely needed.

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APPENDIX A

ORMAL SEASONAL OCCURRENCE OF THE RUNS

Because the weir was not in operation for portions of some years, a weighted average could not be taken. The numbers in the runs are available by weeks. The weir counts are added to the commercial catch allowing a 7-day lag for earlier years and an 11-day lag for the later years when the weir was farther upstream. The 7- and 11-day lags were determined by special tagging experiments (unpublished) designed to measure the speed of migration from Karluk Lagoon to the weir sites.

In order to obtain the normal shape of the curve of occurrence the numbers of fish in all years were added for the period May 31 to August 16, since the data for every year were complete for this period. Each year's data were then weighted by the ratio of the run during this period to the 30-year average. This gave each year equal weight in determining the shape of the curve as well as making it possible to determine the correct shape of the ends of the curve where data for some years were lacking (table A–1).

TABLE A–1.—*Seasonal norm of occurrence of the runs in thousands of fish, 1921–50*

Week ending	Total run	Percent	Cumulative percent	Years with data
y 10	4.9	0.28	0.28	1
y 17	4.2	.25	0.53	9
y 24	20.2	1.16	1.69	30
y 31	88.6	5.09	6.78	30
ne 7	178.5	10.26	17.04	30
ne 14	187.0	10.75	27.79	30
ne 21	137.4	7.90	35.69	30
ne 28	86.5	4.97	40.66	30
y 5	51.2	2.94	43.60	30
y 12	44.0	2.53	46.13	30
y 19	56.6	3.25	49.38	30
y 26	85.8	4.93	54.31	30
g. 2	105.6	6.07	60.38	30
g. 9	97.7	5.61	65.99	30
g. 16	86.0	4.94	70.93	30
g. 23	92.2	5.30	76.23	29
g. 30	100.3	5.76	81.99	28
pt. 6	111.5	6.41	88.40	24
pt. 13	84.4	4.85	93.25	22
pt. 20	48.2	2.77	96.02	22
pt. 27	37.7	2.17	98.19	21
t. 4	21.6	1.24	99.43	17
t. 11	10.2	.59	100.02	9
t. 18	0.0			1
Total	1,740.3	100.02		

APPENDIX B

AGE COMPOSITION OF THE RUNS

The list of ages found in the various years (table A–2) may possibly reflect the different interpretations of the scales made by different investigators. The investigations were commenced by Dr. Charles H. Gilbert and Dr. Willis H. Rich (Gilbert and Rich, 1927). They had several assistants in different years and were followed by other investigators. Among those who were at Karluk in various years were Alan Taft, Seymour P. Smith, Merrill Brown, Joseph T. Barnaby (Barnaby 1944), Allan C. DeLacy, W. Markham Morton, Richard F. Shuman, and Philip R. Nelson.

Absence of a minor age group in any particular year does not mean that it may not have been present. None may have been taken in the samples; the few taken may not have been recognized, or the few taken may have been considered as aberrant scales. (Certainly in some years more age groups were found than in others.) This does not necessarily mean that the very minor age groups are invalid. In fact, there is good evidence from the individual pattern of the seasonal run of most groups that they are probably valid.

These minor groups, as shown later, represent such a minor numerical share of the run that their presence or absence can have but slight effect on the interpretation of the data.

For estimating age composition of the runs, samples are available by weeks, but unfortunately there are many weeks, both during the season and at the two ends when samples are not available. Because each age group has its own individual pattern of seasonal occurrence, the practice that has been followed of extrapolating at either the beginning or end of the season by applying the age readings of the nearest available week to the truncated portions of the data can lead to serious discrepancy. It has, therefore, been necessary to determine the normal pattern for each group (fig. A–1).

The method followed was to first determine the average numbers by weeks of an age group for the

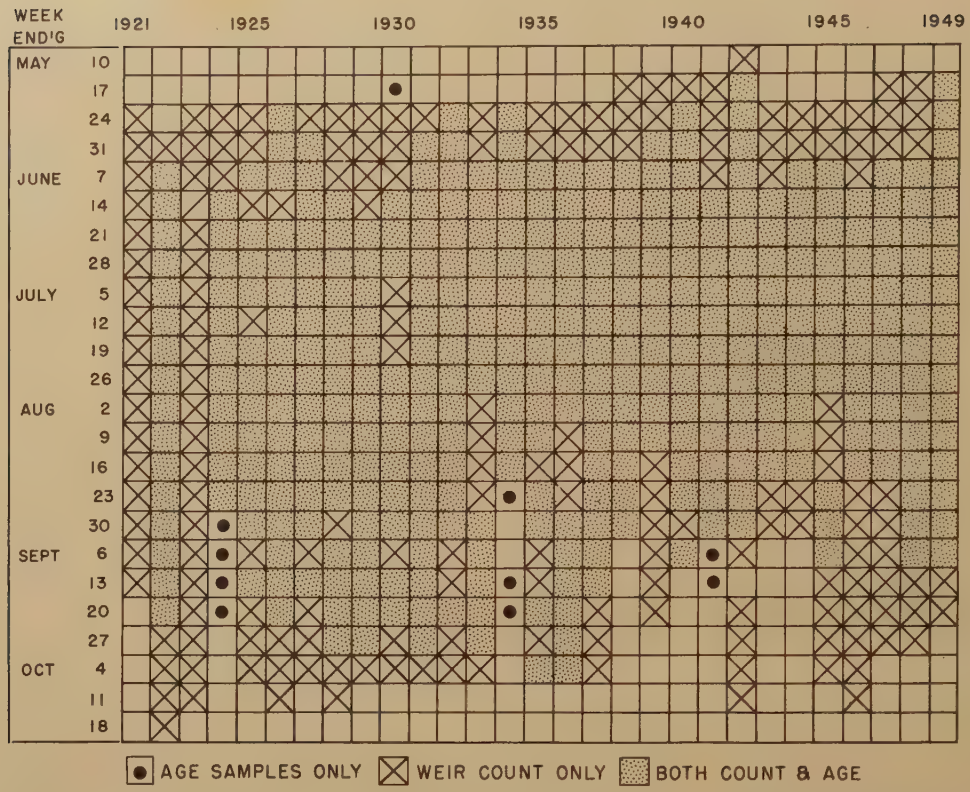

FIGURE A–1.—Availability by weeks for the years 1921–49 of weir counts and age samples of the runs.

TABLE A–2.—*Age groups represented in various years, 1922 and 1924–49*

Year	Age groups																			
	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_4	8_5
1922				x	x	x	x		x	x	x	x		x	x	x		x			
1924			x	x	x	x	x		x	x	x			x	x			x			
1925	x			x	x	x			x	x	x			x	x	x		x			
1926	x			x	x	x	x		x	x	x			x	x	x		x	x	x	
1927	x			x	x	x	x		x	x	x			x	x	x		x	x		x
1928				x	x	x			x	x	x			x	x			x	x		
1929				x	x	x			x	x	x			x	x		x	x			
1930					x	x			x	x	x			x	x		x	x	x		
1931	x			x	x	x			x	x	x			x	x	x	x	x	x		
1932				x	x	x			x	x	x			x	x			x	x		
1933				x	x	x			x	x	x			x	x	x	x	x	x		
1934					x	x			x	x	x			x	x	x		x	x		x
1935		x		x	x	x			x	x	x		x	x	x	x	x	x	x	x	x
1936	x			x	x	x	x		x	x	x		x	x	x	x	x	x	x	x	x
1937		x			x	x			x	x	x			x	x	x	x	x	x		x
1938					x	x			x	x	x			x	x	x	x	x	x		x
1939		x			x	x			x	x	x		x	x	x	x	x	x	x	x	x
1940				x	x	x		x	x	x	x		x	x	x	x	x	x	x	x	x
1941					x	x			x	x	x			x	x		x	x	x		x
1942				x	x	x			x	x	x			x	x		x	x			
1943				x	x	x			x	x				x	x			x	x	x	
1944	x	x		x	x	x			x	x	x		x	x	x		x	x	x	x	x
1945		x			x	x			x	x	x		x	x	x		x	x	x	x	x
1946		x		x	x	x			x	x	x		x	x	x		x	x	x	x	x
1947		x			x	x			x	x	x			x	x		x	x		x	
1948					x	x			x	x	x			x	x		x	x	x		
1949					x	x			x	x	x			x	x	x	x	x	x		x
	Times age group found																				
1922–31	4	0	1	8	9	9	4	0	9	9	9	1	0	9	9	5	3	9	5	1	
1932–40	1	3	0	5	9	9	1	1	9	9	9	0	4	9	9	8	7	9	9	4	
1941–49	1	4	0	4	9	9	0	0	9	9	8	0	3	9	9	1	8	9	7	7	
All years	6	7	1	17	27	27	5	1	27	27	26	1	7	27	27	14	18	27	21	12	

eriod of 10 weeks commencing with the week ding June 14 and finishing with the week ending ugust 16. Complete data on age and total run ere available for all 10 weeks for 18 of the 27 ears with age readings, and the average was based n these 18 years.

The next step was to obtain for each year the tio of the numbers of the age group during as any of the 10 weeks as were available to the umber represented in the same weeks by the urve for the 18-year average.

The reciprocal of this ratio for each year was en used to weight each year's data. By this eans each year was given approximately equal weight in determining the shape of the normal curve of seasonal occurrence for each age group. By summing the numbers for the various years in each week and dividing by the number of years available, a seasonal norm was obtained.

This method was followed for all the major age groups. For several of the minor age groups the data were too few to employ this method, and the numbers were merely summed by weeks and divided by the number of years (for each week) in which ages were taken. The groups so treated were the 3_1, 3_2, 4_1, 4_4, 6_2, 6_5, 7_3, 8_4, and 8_5 groups. The percentage curves of normal seasonal occurrence for each age group are given in table A–3.

ABLE A–3.—*Normal percentage occurrence of each age group by weeks, 1922 and 1924–49*

Week ending	Age group								
	*3_1	*3_2	*4_1	4_2	4_3	*4_4	5_2	5_3	5_4
ay 17	0.00	0.00	0.00	0.00	6.19	0.00	1.81	0.46	0.00
ay 24	.00	.00	.00	.89	4.08	.00	2.61	2.24	.45
ay 31	.00	.00	.38	11.49	2.25	.00	7.51	6.48	2.61
ne 7	.00	.00	1.20	13.10	5.89	.00	21.63	10.39	.91
ne 14	.00	.00	2.97	9.27	4.76	.00	17.11	9.78	1.40
ne 21	.14	.00	5.45	8.50	4.12	.00	11.78	6.96	1.18
ne 28	.14	7.55	5.00	7.31	3.23	.00	8.22	4.19	1.26
ly 5	.14	20.86	3.87	6.19	4.31	.00	4.81	2.70	1.17
ly 12	.97	20.86	3.34	4.83	1.22	.00	4.87	2.41	.74
ly 19	4.35	14.75	7.82	5.39	.98	.00	5.38	3.24	.65
ly 26	16.17	1.80	9.09	4.68	1.75	.00	4.66	5.38	1.13
g. 2	17.34	7.19	7.37	4.12	2.61	.00	2.88	6.68	.98
g. 9	20.33	5.40	6.43	4.07	4.63	.00	1.94	6.42	1.17
g. 16	12.32	5.40	12.10	4.34	3.23	13.11	1.78	5.33	2.59
g. 23	12.49	.00	14.39	3.99	6.98	13.11	1.16	5.25	7.41
g. 30	8.50	5.40	11.84	4.24	10.55	24.41	.85	5.53	9.72
pt. 6	4.70	5.40	5.30	3.09	8.12	16.38	.13	6.95	19.35
pt. 13	2.40	5.40	2.37	2.26	11.48	20.23	.82	5.15	17.55
pt. 20	.00	.00	1.09	1.89	12.99	8.93	.04	2.50	16.88
pt. 27	.00	.00	.00	.35	.64	3.84	.00	1.96	12.85
	99.99	100.01	100.01	100.00	100.01	100.01	99.99	100.00	100.00

Week ending	Age group								
	*6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_4	*8_5
ay 17	0.00	1.75	0.55	0.00	0.00	6.64	0.00	0.00	0.00
ay 24	.00	8.97	.95	.00	14.08	10.01	.00	.00	7.94
ay 31	14.36	11.12	1.95	.00	22.01	12.67	.00	10.38	11.40
ne 7	18.65	18.37	4.48	1.21	15.44	15.22	1.45	14.81	15.37
ne 14	21.45	16.28	4.51	2.01	24.07	10.71	2.42	26.49	12.61
ne 21	10.56	10.83	2.95	2.82	11.92	6.84	1.36	10.38	9.15
ne 28	6.27	6.35	1.93	.00	5.73	3.48	.34	.00	6.56
ly 5	9.08	3.99	1.27	.00	1.83	2.66	.78	4.76	1.90
ly 12	7.26	3.03	1.45	.74	1.45	1.82	.96	2.05	1.90
ly 19	8.42	3.37	2.22	.87	1.13	3.58	1.49	3.89	1.04
ly 26	2.81	3.49	3.73	.00	.94	4.32	2.89	7.89	.86
ug. 2	1.16	3.51	4.87	3.76	.75	4.58	2.84	7.57	2.42
ug. 9	.00	2.83	5.94	.60	.19	4.91	4.23	7.78	2.76
ug. 16	.00	2.05	5.73	3.89	.00	3.49	5.15	.00	3.63
ug. 23	.00	1.45	7.94	9.66	.47	1.98	10.49	.00	5.18
ug. 30	.00	1.06	9.77	4.23	.00	1.87	14.93	.00	7.60
ept. 6	.00	.70	12.94	13.88	.00	1.57	13.05	4.00	6.39
ept. 13	.00	.45	11.11	30.11	.00	2.53	11.32	.00	3.28
ept. 20	.00	.31	7.34	13.88	.00	1.05	21.01	.00	.00
ept. 27	.00	.09	8.37	12.34	.00	.06	5.26	.00	.00
	100.02	100.00	100.00	100.00	100.01	99.99	99.97	100.00	99.99

*Smoothed once by three's.

TABLE A–4.—*Cumulative percentage occurrence of each age group by weeks, 1922 and 1924–49*

Week ending	Age group								
	3_1	3_2	4_1	4_2	4_3	4_4	5_2	5_3	5_4
May 17	0.00	0.00	0.00	0.00	6.19	0.00	1.81	0.46	0.00
May 24	.00	.00	.00	.89	10.27	.00	4.42	2.70	.45
May 31	.00	.00	.38	12.38	12.52	.00	11.93	9.18	3.06
June 7	.00	.00	1.58	25.48	18.41	.00	33.56	19.57	3.97
June 14	.00	.00	4.55	34.75	23.17	.00	50.67	29.35	5.37
June 21	.14	.00	10.00	43.25	27.29	.00	62.45	36.31	6.55
June 28	.28	7.55	15.00	50.56	30.52	.00	70.67	40.50	7.81
July 5	.42	28.41	18.87	56.75	34.83	.00	75.48	43.20	8.98
July 12	1.39	49.27	22.21	61.58	36.05	.00	80.35	45.61	9.72
July 19	5.74	64.02	30.03	66.97	37.03	.00	85.75	48.85	10.37
July 26	21.91	65.82	39.12	71.65	38.78	.00	90.39	54.23	11.50
Aug. 2	39.25	73.01	46.49	75.77	41.39	.00	93.27	60.91	12.48
Aug. 9	59.58	78.41	52.92	79.84	46.02	.00	95.21	67.35	13.65
Aug. 16	71.90	83.81	65.02	84.18	49.25	13.11	96.99	72.66	16.24
Aug. 23	84.39	83.81	79.41	88.17	56.23	26.22	98.15	77.91	23.65
Aug. 30	92.89	89.21	91.25	92.41	66.78	50.63	99.00	83.44	33.37
Sept. 6	97.59	94.61	96.55	95.50	74.90	67.01	99.13	90.39	52.72
Sept. 13	99.99	100.01	98.92	97.76	86.38	87.24	99.95	95.54	70.27
Sept. 20	------	------	100.01	99.65	99.37	96.17	99.99	98.04	87.15
Sept. 27	------	------	------	100.00	100.01	100.01	------	100.00	100.00
	99.99	100.01	100.01	100.00	100.01	100.01	99.99	100.00	100.00

Week ending	Age group								
	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_4	8_5
May 17	0.00	1.75	0.55	0.00	0.00	6.64	0.00	0.00	0.00
May 24	.00	10.72	1.50	.00	14.08	16.65	.00	.00	7.94
May 31	14.36	21.84	3.45	.00	36.09	29.32	.00	10.38	19.34
June 7	33.01	40.21	7.93	1.21	51.53	44.54	1.45	25.19	34.71
June 14	54.46	56.49	12.44	3.22	75.60	55.25	3.87	51.68	47.32
June 21	65.02	67.32	15.39	6.04	87.52	62.09	5.23	62.06	56.47
June 28	71.29	73.67	17.32	6.04	93.25	65.57	5.57	62.06	63.03
July 5	80.37	77.66	18.59	6.04	95.08	68.23	6.35	66.82	64.93
July 12	87.63	80.69	20.04	6.78	96.53	70.05	7.31	68.87	66.83
July 19	96.05	84.06	22.26	7.65	97.66	73.63	8.80	72.76	67.87
July 26	98.86	87.55	25.99	7.65	98.60	77.95	11.69	80.65	68.73
Aug. 2	100.02	91.06	30.86	11.41	99.35	82.53	14.53	88.22	71.15
Aug. 9	------	93.89	36.80	12.01	99.54	87.44	18.76	96.00	73.91
Aug. 16	------	95.94	42.53	15.90	99.54	90.93	23.91	96.00	77.54
Aug. 23	------	97.39	50.47	25.56	100.01	92.91	34.40	96.00	82.72
Aug. 30	------	98.45	60.24	29.79	------	94.78	49.33	96.00	90.32
Sept. 6	------	99.15	73.18	43.67	------	96.35	62.38	100.00	96.71
Sept. 13	------	99.60	84.29	73.78	------	98.88	73.70	------	99.99
Sept. 20	------	99.91	91.63	87.66	------	99.93	94.71	------	------
Sept. 27	------	100.00	100.00	100.00	------	99.99	99.97	------	------
	100.02	100.00	100.00	100.00	100.01	99.99	99.97	100.00	99.99

APPENDIX C

ESTIMATION OF NUMBERS AND OF AGE COMPOSITION OF THE ANNUAL RUNS

Portions of the escapement were not counted during 7 of the years, and scale samples for ages are missing for varying proportions of most seasons. Because each age group has its own pattern of seasonal occurrence a special procedure was evolved to resolve this problem. It was decided that grave errors in estimation would result from extrapolating age readings from the first or last week sampled by applying them directly to the earlier or later portions of the run. Neither have we used any estimates of the run not based on actual catches and on counts at the weir. The percentage of runs without age readings or weir counts, or both, are as follows:

9-year periods	Before July 12	After July 12	Total
1922, 1924–31	27	13	18
1932–40	4	30	16
1941–49	20	34	26
Total	16	23	19.5

In individual years the spring portion lacked as high as 74 percent of the data and the fall portion as high as 71 percent. For this reason the estimates of the age composition that we have derived, as well as the numbers of fish in some of the years when the weir count was incomplete, differ in some degree from previously published material.

Because of the sharp difference in age composition between the beginning and the end of the runs, the portions with missing data were estimated separately for the two halves of the season and divided at the end of the week ending July 19.

The method of estimation, while time consuming, is relatively simple. Utilizing tables A–3 and A–4, the percentage was obtained of each age group that would normally occur during the portion of the year for which age and enumeration data were available. Next the percentage was obtained of each age group that would normally occur during the period up to July 19 for which age data were lacking. The number of fish was then computed (for each age group) that would be required (on the basis of the number and percentage with data) to bring that age group up to normal.

For example, suppose 75 percent of the 6_4 group normally should occur during that portion of the season for which ages and counts of the run were available. Then suppose 15 percent should normally occur during the portion of the season up to July 20 for which data are not available. Further let us suppose that the 75 percent represents 200,000 fish. Then 200,000 times 15/75 or 40,000 would be the number estimated to occur during the early season.

The estimates of the missing numbers were made for each age group and totaled. This total was then divided by the total enumeration (weir count plus catch) for the period without age data and the estimated total of each age group was then decreased or increased in proportion to this ratio. By this means the total of all ages was made to agree with the actual enumeration.

The same procedure was followed with the portion of the season following July 19, except that for the 7 years without full enumeration the uncorrected estimates of the numbers of each age group were used for the portion of the season that lacked an actual tally, as we feel that this objective method should give a more accurate estimate than any used previously. The estimates are given in table A–5. The figures were not rounded off because of the incidence of many minor age groups.

TABLE A–5.—*Estimated numbers of each age group of sockeye in the annual runs to the Karluk River, 1922 and 1924 to 1949*

Year of run	Age groups									
	3_1	3_2	4_1	4_2	4_3	4_4	5_2	5_3	5_4	6_2
1922			896	6,451	8,750	1,390	3,168	691,889	20,180	
1924			177	6,131	51,616		5,998	1,392,627	59,482	
1925	12,824		3,710	37,920	152,187		5,369	1,985,213	70,902	
1926	8,115		18,760	97,462	21,013	1,064	49,342	3,960,107	10,224	
1927	138		1,682	3,443	41,329	370	91,568	1,139,945	46,273	
1928			309	9,749	6,066		3,812	1,205,915	5,087	
1929			223	5,728	5,722		5,350	386,013	2,988	
1930				807	40,382		8,493	668,420	135,089	
1931	312		115	18,334	8,961		5,823	791,366	48,736	
1932			2,029	17,909	11,780		19,229	750,577	18,982	
1933			1,245	8,715	7,864		37,339	979,393	14,892	
1934				63,137	5,641		35,893	711,766	61,576	
1935		68	3,012	62,301	57,041		40,573	503,766	50,201	1,5
1936	270		691	22,473	38,788	166	82,761	1,708,473	44,539	7
1937		242		14,023	51,029		23,439	1,589,153	43,163	
1938				57,233	14,099		32,320	1,326,449	4,336	
1939		324		1,249	8,503		20,864	357,728	38,842	
1940			190	7,522	7,531		2,931	418,914	64,477	1
1941				6,985	13,067		7,141	834,807	38,897	
1942			1,036	9,589	25,056		10,097	600,700	10,590	
1943			7,950	10,684	15,935		33,749	949,714		
1944	1,310	56	756	11,613	3,597		49,307	796,302	14,188	6
1945		298		12,185	2,003		127,450	263,751	687	2
1946		484	197	5,284	1,376		22,981	122,794	7,500	5
1947		80		4,995	17,170		12,761	158,208	29,118	
1948				1,090	6,427		6,848	1,002,605	926	
1949				809	3,806		1,439	596,380	1,136	

It was now possible to compile a table showing e total run divided into catch and escapement nd of the adults that returned in later years as a sult of the spawning of each year's escapement able A–6).

ABLE A–5.—*Estimated numbers of each age group of sockeye in the annual runs to the Karluk River, 1922 and 1924 to 1949*—Continued

Year of run	Age groups							
	6_3	6_4	6_5	7_3	7_4	7_5	8_4	8_5
2	244,057	79,159	619	.....	1,440	.....	.....	.....
4	83,655	344,990	.....	.....	8,751	.....	.....	.....
5	122,721	540,873	969	.....	11,312	.....	.....	.....
6	242,792	471,727	2,273	.....	32,308	4,619	194	.....
7	119,029	129,311	640	.....	10,369	2,734	.....	169
8	578,612	253,933	.....	.....	29,087	2,094	.....	.....
9	340,107	361,192	.....	4,077	16,700	.....	.....	.....
0	189,581	193,037	.....	25	17,950	215	.....	.....
1	104,767	628,878	1,446	244	14,764	1,253	.....	.....
2	71,846	471,048	.....	.....	40,840	7,761	.....	.....
3	286,175	446,593	563	772	19,737	9,711	.....	.....
4	783,531	639,920	.....	.....	63,206	3,982	.....	1,016
5	296,785	370,929	1,386	2,503	115,482	24,504	594	263
6	195,249	270,434	48	1,243	70,428	15,872	397	443
7	178,261	388,637	4,786	372	17,937	23,460	.....	1,498
8	362,051	370,332	316	119	22,562	23,896	.....	597
9	548,439	149,310	1,998	1,657	80,563	4,680	898	353
0	301,355	405,807	1,187	3,808	49,276	4,387	142	66
1	192,065	473,348	.....	2,458	57,231	2,708	310	402
2	115,449	274,837	.....	1,109	86,652	.....	.....	886
3	397,851	245,617	.....	.....	62,436	2,387	876	.....
4	359,434	125,103	.....	2,301	43,218	1,021	1,062	343
5	665,600	178,251	.....	3,421	76,984	1,334	2,546	226
6	212,614	204,336	.....	6,763	82,223	2,241	412	292
7	156,163	182,641	.....	490	31,962	.....	1,413	.....
8	125,916	200,865	.....	3,436	60,049	1,839	.....	.....
9	230,855	230,986	374	1,219	68,850	3,226	1,469	450

ABLE A–6.—*Catches, escapements and returns from escapements in thousands of fish, 1919–49*

Year of run	Total run	Catch	Escapement	Return
19	.....	1,090	.....	[1] 2,160
20	.....	1,369	.....	2,849
21	(?)3,143	1,643	(?) 1,500	4,494
22	1,058	658	400	2,282
23	1,425	730	695	1,990
24	1,953	891	1,063	809
25	2,944	1,323	1,621	1,607
26	4,920	2,386	2,534	1,461
27	1,587	715	872	1,618
28	2,095	1,001	1,094	2,630
29	1,128	227	901	1,587
30	1,254	167	1,087	1,172
31	1,625	752	873	2,578
32	1,412	674	738	2,538
33	1,813	845	968	2,186
34	2,370	919	1,450	1,261
35	1,531	655	876	1,250
36	2,453	1,078	1,375	1,353
37	2,336	1,071	1,265	1,334
38	2,214	984	1,230	1,587
39	1,215	509	706	1,831
40	1,268	451	816	858
41	1,629	698	932	575
42	1,136	507	629	[2] 607
43	1,727	806	921	[3] 1,495
44	1,410	641	769	.....
45	1,335	676	659	.....
46	670	228	442	.....
47	595	110	485	.....
48	1,410	657	753	.....
49	1,141	450	691	.....
um for period 1921—43	44,236	19,690	24,546	39,103

[1] Plus 4-year-olds.
[2] Plus 8-year-olds.
[3] Plus 7 and 8-year-olds.

APPENDIX D

ESTIMATION OF ESCAPEMENT

The sockeye salmon fishery at Karluk commenced with the salting of salmon in 1867, but the first cannery was established in 1882 (Moser 1899). For 6 years, from 1882 to 1887 only one cannery operated at Karluk and the pack increased each year.

Three canneries operated in 1888 and five in 1889 (Gilbert and Rich, 1927). Up to this time all fishing had been conducted only in the lagoon and in the river inside the sand spit at the mouth, but commencing in 1889 most of the fishing was carried on outside of the river. For the next few years the catch was limited to a large extent by the capacity of the canneries. This is probably one reason why the catches during the years from 1888–94 were fairly uniform in quantity.

There is some evidence that even during this period the large catches were being made (at least in some years) at the expense of the escapement. Shuman (1950) states,

> While catches are subject to many variables, such as fishing intensity, availability, and economic conditions, it is believed that at Karluk they are a reasonably good index of abundance, and it is further believed that the escapements (spawning populations) have decreased proportionately to the decrease in abundance. By *a posteriori* reasoning, the escapements prior to the advent of commercial fishing must have been at least 3 million fish annually. In the first 10 years of operation of the Karluk weir (1921–30) the mean annual escapement was 1.2 million, while for the past 3 years the mean escapement was only 0.4 million.

Prior to the advent of commercial fishing the escapement and the total run are practically one and the same. After 1888 when the fishery was well established the escapement in order to bear the same relation to the catch in earlier years that it did after the weir was established would have had to be larger than the commercial catch. This would mean a total run (in the 1888–93 period at least) of about 6 million fish, so that prior to the advent of commercial fishing the escapement would have been about 6 million.

There is reason to seriously doubt that the runs attained such proportions, except perhaps in a very abnormal year. Rather we are inclined to the view that during the earlier years of the fishery, when fishing was practically unrestricted, the

total catch represented a much greater share of the total run than in any year since 1924.

The largest run since 1924 was in 1926. Because of fishing restrictions the commercial take was limited to 2,386,000 fish and 2,534,000 salmon passed the weir toward the lake. Rich visited the lake and states (Gilbert and Rich, 1927),

> Particular attention was given to the spawning of the adult fish, which was made especially interesting and important by the remarkably fine run and escapement of 1926. The spawning escapement was the best in many years, and in all probability was the best that has ever been observed by the few white men who have visited the lake.

Observers visited the lake in a number of prior years: Tarleton H. Bean in 1889, Cloudsley Rutter and M. H. Spaulding (Chamberlain 1907) in 1903, Ward T. Bower in 1911, E. M. Ball in 1917, Henry O'Malley and Charles H. Gilbert in 1919 and 1921, C. H. Gilbert, W. H. Rich, W. P. Studdert, and Fred Lucas in 1922, and Fred Lucas in 1924.

If we assume that Rich's statement is correct, then it is apparent that escapements in earlier years were proportionately smaller than in more recent years. Some measure of this can be gained by comparing the notes of Cloudsley Rutter (Chamberlain 1907, p. 100) with those of Shuman (1950). In 1947 Shuman counted 15,000 salmon (14,826) in Moraine Creek. In 1903 Rutter counted 22,000 (21,756) in the same creek. Since the total escapement in 1947 was 485,000 the escapement of 1903 can be roughly estimated as 22/15 of 485,000 or 711,000. The catch in 1903 was 1,320,000 which would make the escapement only 35 percent of the total run. This is, of course, assuming, which may not be warranted, that spawning in Moraine Creek is representative of the entire run.

A similar situation existed in the sockeye fishery of the Fraser River (Rounsefell 1949). The escapements in the Fraser River from 1894 to 1921 (seven 4-year cycles) averaged 18 percent of the runs, whereas from 1922–45 (six 4-year cycles) they averaged 27.4 percent of the run. Escapements during the earlier period averaged only 65 percent of escapements after 1921. It will be noted that the Fraser fishery was building up slowly with an escapement of slightly more than 25 percent of the runs, which is one-half of the Karluk escapement of recent years, under which the Karluk fishery has continued to decline.

Another factor, possibly minor, that until now has been ignored in discussing escapements is the role of the Karluk hatchery, which was operated in 1891 and again from 1896 to 1916. It was in operation during the same era that sockeye fry were planted in the Fraser River at New Westminster. Results from the planting of fry at the mouth of the Karluk River undoubtedly were equally nonproductive. However, the Karluk run was much smaller than that of the Fraser so that salmon taken out of the escapement for the hatchery may have made a significant reduction in the escapements of the poorer years.

The chief loss from the hatchery was not so much in the numbers of salmon actually stripped as in the large numbers of fish that were killed in handling or that died in the corrals in which they were held for ripening. From various sources table A–7 has been compiled. The number of eggs stripped is shown a year later than are the other statistics as they were reported by fiscal years commencing July 1, and few eggs were ever taken in June. It is obvious that the numbers of salmon captured and held for spawning greatly exceeded the number surviving to be stripped. Bower (1912, p. 75) says,

> There is a tremendous mortality of fish held in corrals and ponds, due no doubt to crowding so many fish together in a limited space, and the loss is particularly heavy during the latter half of July when the water warms up. The season of 1910, the last for which complete statistics are available, is typical of conditions at Karluk. From June 7 to August 10, 1910, a total of 85,623 adult salmon were impounded. Of these fish a total of 42,174, or nearly 50 percent, died and were of no use whatsoever.

In order to determine certain population parameters it was necessary to postulate the escapements prior to the establishment of the counting weir in 1921. Any empirical estimation is subject to legitimate criticism, but the decline in the fishery is of such magnitude that any reasonable estimate will suffice for our purpose.

In constructing table 6 our calculations from the weir counts and age samples were utilized from 1921–49. For prior years we have estimated escapement as 53.85 percent of the catch (based on 35 percent escapement of the total run). An estimate of fish impounded for the hatchery as shown in table A–7 was not subtracted from the estimated escapement.

Table A–7.—Artificial propagation at Karluk

Year (calendar)	Reported number of eggs per female stripped	Number of females stripped	Number of males stripped	Total number stripped	Total impounded	Number of eggs in millions (fiscal years)	Estimated number of eggs per female impounded (calendar years)	Estimated number of salmon impounded
								4,699
						2.5		
								6,015
		2,285		3,348	6,640	3.2	1,280	6,640
						8.5		8,459
		2,837				4.5		19,737
		5,524			79,753	10.5	242	79,753
						19.3		61,654
						32.8		43,985
						23.4		52,820
						28.1		85,526
						45.5		69,361
					18,000	36.9	2,150	18,000
						38.7		89,850
						47.8		75,752
						40.3		84,962
				43,449	85,623	45.2	579	85,623
	2,826	14,516	14,770	29,286		49.6		77,068
						41.0		85,714
	3,109					45.6		65,038
	2,542					34.6		56,767
	2,620					30.2		77,256
						41.1		1,880
						1.0		
erage number eggs per female impounded							1,063	
erage number of eggs per salmon impounded (1063/2)							532	

APPENDIX E

RAINFALL AND SPAWNING SUCCESS

For the Skeena River sockeye, Brett (1951) tempted to determine the effect of precipitation August and September on success of reproduction for the 1920–34 period. He used multiple rrelation with four variables: seeding (estiates of numbers spawning), precipitation, proiction (returning adults taken in catch at rious ages from each seeding), and catch (in e brood year). His "seeding" is a ranked timate-of-escapement that is not significantly rrelated with catch in the brood year (r is 8 and P.05 is .51). Precipitation and production gave a correlation of .56 (P of .05 is .51). recipitation and production with seeding held onstant gave a partial correlation of .64 (P of 05 is .53, P of .01 is .66).

Brett has assumed linear relations both between e returns (production) and number of spawners "seeding" or catch), and also between rainfall nd returns. Analysis of his data (fig. A–2 and –3) shows that the ranked seeding is probably a very poor estimate of escapement. The second portion of figure A–2 shows that the catch in the brood year is probably a good relative measure of escapement since the $\log_{10}$ production/catch in brood year shows a high negative correlation with catch in the brood year, $r=-.79$ and P of .01 is .64. The lower portion of figure A–2 shows the reproduction curve resulting from this relationship.

The residuals of $\log_{10}$ production/catch in the brood year versus catch in the brood year are shown in figure A–3 as the ordinate and inches of rainfall in August and September as the abscissa. The correlation is .59 with $P.05=.51$ and $P.01=.64$. However, if we exclude 1920 data the correlation is very high .75 with $P.01=.66$. The curve shown in figure A–3 is calculated without 1920. It would appear that the function is probably curvilinear, and, as the Karluk data seem to indicate, the production reaches a maximum and then declines if rainfall is excessive.

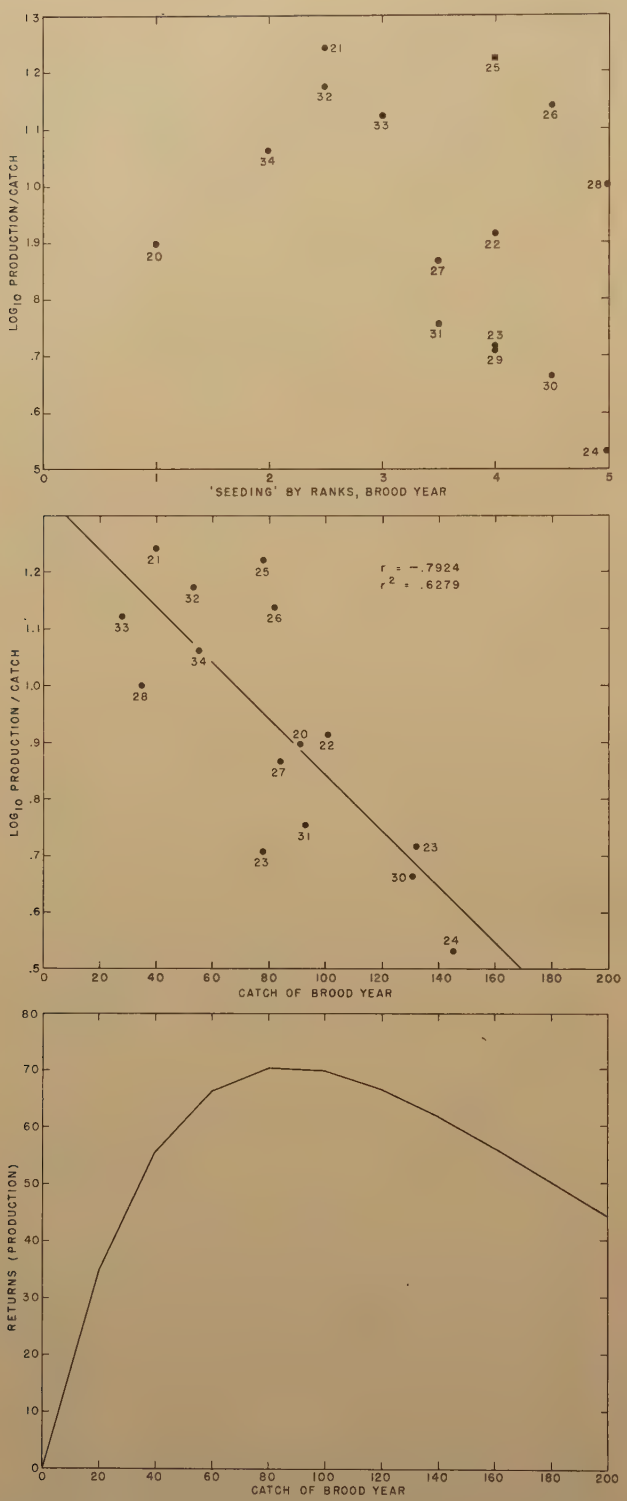

FIGURE A–2.—Relationship between spawners and returns for the Skeena River.

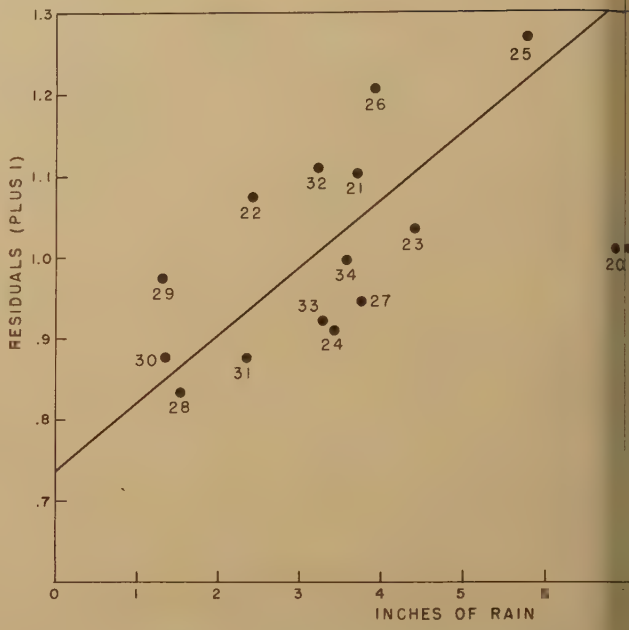

FIGURE A–3.—Relation between late summer rainfall and relative success of spawning as given by the residuals of log production/catch of brood year versus catch of brood year for the Skeena River.

APPENDIX F

DATA ON CULTUS LAKE SMOLT MIGRATIONS AND RETURNS

TABLE A–8.—*Analysis of data on smolt migrations and returns from sockeye of Cultus Lake*

[Data from Foerster 1954]

Year of smolt migration	Number of smolts (-000)	Average length cm.	Average weight gm.	Returning adults in escapement (—00)
1927	250	10.07	11.0	64
1928	336	8.08	5.1	109
1929	2,460	6.86	3.1	398
1930	104	10.70	12.8	48
1931	365	9.08	7.3	76
1932	779	9.02	7.3	202
1933	1,556	7.22	3.7	161
1934	184	8.66	8.4	85
1935	324	9.26	8.2	27
1936	498	9.80	8.9	288
1937	3,112	8.42	5.8	756
1938	1,640	8.8	7.0	736
1939	217	10.5	12.8	145
1940	1,375	9.9	9.7	411
1941	3,979	6.3	2.7	122
1942	1,752	8.1	5.4	141
1943	694	9.2	7.8	52
1944	2,012	8.9	7.5	373

APPENDIX G

CALCULATION OF NUMBER AND BIOMASS OF KARLUK SMOLT MIGRATIONS

The length-weight curves in table A–9 are derived from linear least square fits of the logarithms of length and weight. For Karluk the average lengths and weights for each centimeter length interval for three weekly sampling periods were used. In fitting, these averages were weighted by the numbers involved.

In constructing table A–10 the 2- and 5-year emigrants, which usually account for about 2 to 5 percent of the returning adults were omitted because of the lack of adequate data on their survival. The length for the week ending June 7 was used because it was sampled in all years, and is about midway in the smolt migration. The average weights in grams for the lengths given were from figure A–4.

The number of smolts of each age leaving the lake was estimated from the number of adults surviving, by utilizing the smolt to adult survival rates determined from marking experiments. Barnaby (1944) found for 6 years that the rates for all smolts were 20.8 percent (this year with incomplete returns), 22.3, 21.0, 23.6, 20.5, and 17.5 percent. For the 3-year smolts the survival rate was 17.4 percent and for smolts leaving in their fourth year the rate was 25.7 percent.

Table A–11 shows the 3- and 4-year smolts combined by the years in which they left the lake rather than by brood year. This has been done in order to assess the total biomass of smolts leaving the lake in any one year (minus the 2- and 5-year smolts).

TABLE A–9.—*Length and weight of seaward-migrant sockeye (fork length in millimeters, weight in grams)*

Length (mm.)	Weight		
	Karluk Lake [1] (gms.)	Cultus Lake [2] (gms.)	Babine Lake [3] (gms.)
60		2.21	
65		2.76	
70		3.47	
75		4.29	3.94
80		5.22	4.90
85		6.29	6.01
90		7.49	7.28
95		8.85	
100	9.01	10.35	
105	10.46	12.02	
110	12.06	13.87	
115	13.81		
120	15.73		
125	17.82		
130	20.08		
135	22.53		
140	25.18		
145	28.04		
150	31.10		
155	34.32		
160	37.86		
165	41.60		
170	45.56		

[1] Based on 1031 specimens, May 28–June 13, 1936.
[2] Based on average lengths and weights of total migrations 1927–44 (Foerster 1954).
[3] Based on average lengths and weights of smolts in second year 1950–53 (Dombroski 1954).

TABLE A–10.—*Size, number, and weight of 3- and 4-year smolts from each brood year, 1922–37*

Brood year	Size of smolts migrating week ending June 7				Adults from brood year according to migrant age		Estimated number of smolts leaving lake		Total biomass of smolts	
	Length (mm.)		Weight (gms.)		Age 3 (–000)	Age 4 (–000)	Age 3 [1] (–000)	Age 4 [2] (–000)	Age 3 (Metric tons)	Age 4 (Metric tons)
	Age 3	Age 4	Age 3	Age 4						
22	135.6	145.9	22.8	28.5	1,744	318	10,023	1,237	228.52	35.25
23	135.8	145.9	22.9	28.5	1,587	385	9,120	1,498	208.85	42.69
24	132.6	143.4	21.2	27.3	582	210	3,345	817	70.91	22.30
25	129.8	145.7	19.9	28.4	779	805	4,477	3,132	89.09	88.95
26	130.1	140.1	20.0	25.2	904	540	5,195	2,101	103.90	52.95
27	126.7	139.7	18.5	25.0	1,046	529	6,011	2,058	111.20	51.45
28	129.9	142.9	20.0	26.8	1,777	771	10,212	3,000	204.24	80.40
29	131.8	147.2	20.9	29.5	1,018	503	5,850	1,957	122.26	57.73
30	137.7	147.8	23.9	29.6	705	339	4,052	1,319	96.84	39.04
31	138.9	153.7	24.8	33.3	1,944	457	11,172	1,778	277.07	59.21
32	142.0	142.6	26.3	26.6	1,992	494	11,448	1,922	301.08	51.13
33	132.7	125.8	21.3	18.2	1,930	203	11,092	790	236.26	14.38
34	119.5	130.2	15.5	20.1	676	502	3,885	1,953	60.22	39.26
35	120.2	142.9	15.7	26.8	621	625	3,569	2,432	56.03	65.18
36	128.7	142.1	19.4	26.4	958	377	5,506	1,467	106.82	38.73
37	131.8	138.3	21.0	24.3	1,014	302	5,827	1,175	122.37	28.55

[1] Times reciprocal of 17.4 percent or 5.747.
[2] Times reciprocal of 25.7 percent or 3.891.

TABLE A–11.—*Number and total weight of smolts leaving Karluk and Cultus Lakes in various years, 1926–44 (weight in metric tons)*

[Number in thousands]

Year of seaward migrations	Karluk Lake [1]				Cultus Lake [2]	
	Weight			Number	Weight	Number
	Age 3	Age 4	Ages 3 and 4			
1925	222.52					
1926	208.85	35.25	244.10	10,357		
1927	70.91	42.69	113.60	4,843	2.75	250
1928	89.09	22.30	111.39	5,294	1.72	336
1929	103.90	88.95	192.85	8,327	7.63	2,460
1930	111.20	52.95	164.15	8,112	1.33	104
1931	204.24	51.45	255.69	12,270	2.67	365
1932	122.26	80.40	202.66	8,880	5.69	779
1933	96.84	57.73	154.57	6,009	5.79	1,566
1934	277.07	39.04	316.11	12,491	1.54	184
1935	301.08	59.21	360.29	13,226	2.66	324
1936	236.26	51.13	287.39	13,014	4.43	498
1937	60.22	14.38	74.60	4,675	18.05	3,112
1938	56.03	39.26	95.29	5,522	11.48	1,640
1939	106.82	65.18	172.00	7,938	2.78	217
1940	122.37	38.73	161.10	7,294	13.34	1,375
1941		28.55			10.74	3,979
1942					9.46	1,752
1943					5.41	694
1944					15.09	2,012
Sum			2905.79	128,252	122.56	21,647
Average			193.72	8,550	6.81	1,203
1927–1935:						
Sum					31.78	6,368
Average					3.53	708
1936–1944:						
Sum					90.78	15,279
Average					10.09	1,698

[1] Omitting the smolts leaving in second and fifth years, usually 2 to 5 percent.
[2] Calculated from Foerster (1954, table 1).

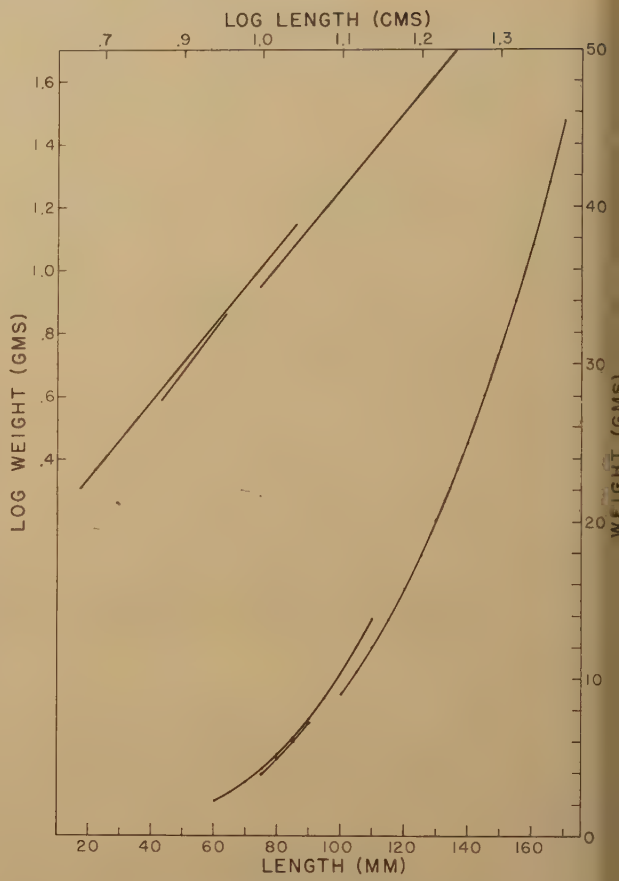

FIGURE A–4.—Length-weight curves for sockeye smolts from Karluk, Cultus, and Babine Lakes.

TABLE A–12.—*Comparison of Karluk and Cultus Lakes* [1]

Item	Karluk	Cultus
Area:		
Square miles	16.04	2.42
Acres	10,266	1,550
Watershed: Square miles	108.67	32.0
Annual rainfall:		
Kodiak 1916–41, inches	57.2	
1933–35, inches		61.8
Volume of lake: Acre feet	1,556,851	175,470
Total precipitation on watershed: Acre feet	331,749	105,472
Minimum outlet flow:		
August 1928 (7 cu. meters), c. f. s	247	
Late summer (½ cu. meter), c. f. s		18
Annual number of smolts:		
Average per acre	833	776
Maximum per acre	1,288	2,567
Biomass of migrating smolts:		
Metric tons, average	193.7	6.8
Kilos per acre, average	18.8	4.4
Pounds per acre, average	41.4	9.7
Kilos per acre, maximum	35.1	11.6
Pounds per acre, maximum	71.1	23.5
Ratio of lake volume to total precipitation on watershed	4.7	1.7

[1] Physical data for Cultus Lake from Ricker (1937b).

APPENDIX H

COMPARISON OF ALTERNATE METHODS FOR DERIVING RESIDUALS OF RETURN ON ESCAPEMENT

In the section of this report dealing with the effect of climate on success of reproduction the residuals of return on escapement employed are derived from the formula (letting y equal return and x equal escapement):

$$y/x = a - b \log x \qquad (1$$

This corresponds to:

$$y = (a - b \log x)x \qquad (2$$

which can be written (See fig. 19) as:

$$\log y = x\epsilon^{a-b \log x} \qquad (3$$

The question was raised by reviewers of the aft of this report as to whether use of a ratio in ting (formula 1) may yield biased residuals. This point has been tested by comparing the siduals derived from other formulae with those rived from formula 1 above. Since it was ggested that it might be advantageous to rrect for time in years because of the declining n, a time factor was used in some of the tests. Letting y equal return, x equal escapement and equal time, three regressions were calculated:

$$\log y = a + b \log x + b_{y_{1.2}}\, t + b_{y_{1.3}}\, t^2 \qquad (4)$$

$$\log y = a + b \log x + b_{y_{1.2}}\, t \qquad (5)$$

$$\log y = a + b \log x \qquad (6)$$

The residuals of log y on log x were then calulated for each formula (holding t and t^2 at $\bar{t}$ and in the appropriate formulae). These residuals were then compared with those derived from formula 1 above. The period 1887–1923 was used to give comparisons with figures 5, 6, and 19.

Comparison of residuals of y (formulae 4, 5, and 6) on residuals of y (formula 1):

Formulae	r	r^2	Syx
4 and 1	0.8884	0.789	0.088
5 and 1	.9290	.863	.070
6 and 1	.9342	.873	.069

It will be noted that the correlations between the sets of residuals are all high, the highest occurring between residuals of formulae 6 and 1. These are plotted in figure A–5. There appears to be a slight tendency toward curvilinearity in their relation as shown by the empirical curve drawn through the grouped means. The standard error of estimate about the empirical curve is

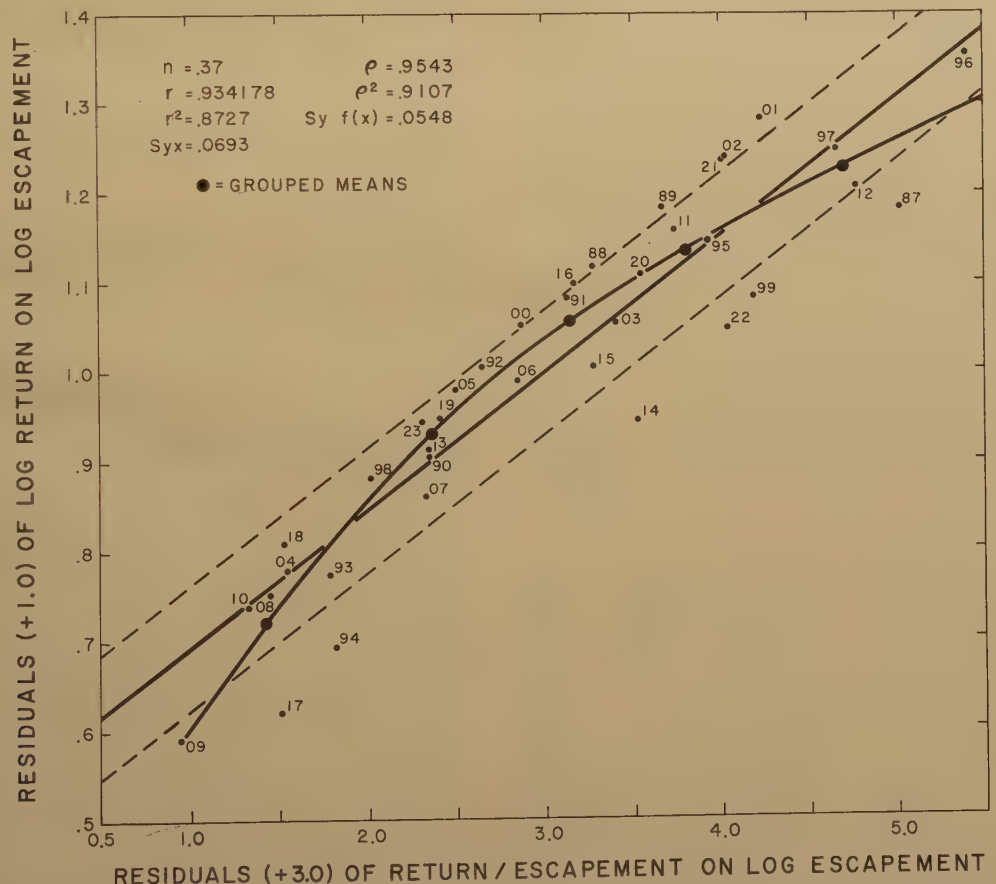

FIGURE A–5.—Comparison of residuals of return on escapement derived by two methods.

.055 compared to 0.69 for the linear regression. The index of correlation, P, for the empirical curve is 0.9543 compared to the linear correlation coefficient of 0.9342. However, the difference between the two (Fisher, 1936, p. 206), 0.188 is less than its standard deviation, 0.242, and hence not statistically significant.

APPENDIX I

RELATION OF KODIAK AND KARLUK TEMPERATURES

Because the only extended series of records of climatic conditions were taken at the town of Kodiak, they were employed in this study so that the degree of association between Kodiak and Karluk conditions is important in evaluation of the data. That the daily temperatures of the air and surface of the sea at various points around Kodiak Island are closely associated was shown by Rounsefell (1930) from a series of temperatures from April through September, 1926.

Water temperatures for Karluk Lake were published for certain dates by Juday et al. (1932) for the 1926–30 period and by Barnaby (1944) for 1935 and 1936. The summer temperatures for these years for surface and 10-meter depths are shown in table A–13. These have been correlated (fig. A–6) with Kodiak air temperatures for a 30-day period ending on the date the water temperature was taken. Both series of water temperatures show a high significant correlation with the air temperature. As expected the surface water temperature is more variable than the temperature at 10 meters.

This indicates that average monthly air temperatures at Kodiak are a useful and fairly reliable indication of Karluk water temperatures.

TABLE A–13.—*Comparison of Kodiak and Karluk summer temperatures, 1926–36* [1]

Date			Karluk Lake temperature		Kodiak air temperature 30-day period to date shown [2]
Year	Month	Day	Surface	10 meters	
			° F	° F	° F
1926	August	15	60.08	56.30	56.80
1927	July	19	52.34	49.46	51.21
Do	August	13	51.98	50.54	52.77
1928	July	10	50.36	47.30	50.67
Do	September	3	49.46	49.46	53.02
1929	July	9	55.76	49.10	51.18
Do	September	8	53.60	52.70	55.48
1930	July	12	49.64	46.94	50.28
1935	June	28	51.80		49.72
Do	July	11	52.88		51.52
Do	do	30	53.42		54.50
Do	August	13	53.96		54.80
Do	September	6	54.86		54.36
1936	June	28	56.48		55.08
Do	July	11	53.96		57.61
Do	do	18	56.30		58.64
Do	August	7	62.78		59.65
Do	do	13	59.90		59.01
Do	do	27	59.00		57.52
Do	September	9	55.86		55.16

[1] Karluk temperatures 1926–30 from Juday et al. (1932), 1935–36 from Barnaby (1944).
[2] Derived from mean monthly temperatures weighted by number of days falling in each month.

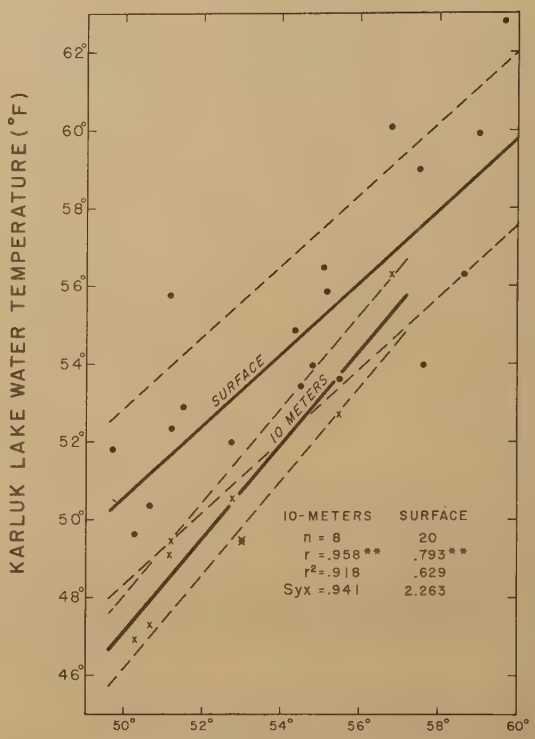

FIGURE A–6.—Comparison of Karluk Lake water temperatures with Kodiak air temperatures for the preceding 30-day period.

APPENDIX J

RELATION OF AGE OF SMOLTS AT MIGRATION TO TEMPERATURE, SIZE, AND NUMBER

The question of an increase in the average age of smolts is a troublesome one. It was shown that the broods with larger returns have a larger proportion of younger fish, but this can perhaps be explained by the additional mortality resulting from a greater age at maturity.

It has been suggested by some authors that an increased age of smolt at Karluk has been caused by lack of sufficient fertility of the lake. However figure 28 showing the strong linear relation between numbers and biomass of smolt migrations refutes this suggestion.

The question has been raised as to whether the creased smolt age has been accompanied by a ecrease in smolt size. Figure A–7 shows that the verage length of the 1922–37 broods (migrating their third year from 1925–40 and in their urth year from 1926–41) at time of migration om the lake varied widely with no apparent end (r for time and length equals —0.29 and is ot significant).

In an attempt to answer the question as to what uses a smolt to migrate we have calculated a ultiple regression in which

y=the ratio of smolts migrating in their third year to smolts of the same brood migrating in their fourth year (columns 8 and 9, table A–10).

x_1=length of smolts migrating in their third year (column 2, table A–10).

x_2=mean June–July air temperature at Kodiak year of migration.

x_3=total numbers of 3 year smolts and 4 year smolts leaving lake (from 2 different broods, column 5, table A–11) year of the migration.

The resulting correlations are:

Ratio 3/4 smolts of same brood (Y)	3-year length (X_1)	June–July temperature (X_2)	Number 3 and 4 smolts migrating (X_3)
rrelations of Y with X's	0.4534	0.9152**	0.6705**
andard regressions of Y on X's	.0583	.7966**	.2600

R=0.9365**.

However, examination of table A–14 shows that he apparent high correlation with temperature is rgely due to the extremely high 3/4 smolt ratio r the 1933 year class and the correspondingly treme temperature of 58.20° F. It would pear that this extreme temperature had some hysiological effect which caused a very much eavier migration than normal for the length, eatly reducing the length-ratio correlation.

The distinct possibility of such a physiological fect is substantiated by the work on temperature lerance in Pacific salmon by Brett (1952). He owed (p. 300, fig. 22) that young sockeye climated at 5° C. had a preference (modal pref-

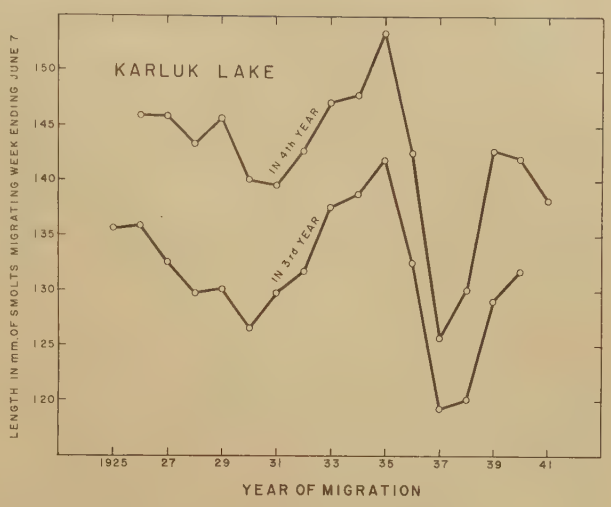

FIGURE A–7.—Lengths of Karluk smolts migrating in their third and fourth year.

erence) of 10 to 11° C., and even for young sockeye acclimated at 10° C. the modal preference was 12 to 13° C. with the upper limit of one standard deviation at about 14.5° C. This upper limit of 14.5° C. is almost exactly equivalent to the 58.20° F. the 3-year-olds of the 1933 brood encountered in June and July of 1936.

Since this temperature was far above any of the other years we recalculated the multiple regression

TABLE A–14.—*Factors influencing age of smolts at time of seaward migration*

Year of spawning	Ratio of smolts migrating in year 3 to those migrating in year 4 (Y)	Length of 3-year smolts (X_1)	Mean June-July Kodiak temperature year when 3-year smolts migrate (X_2)	Number of 3-year and 4-year smolts migrating in year 3-year smolts migrate (X_3)
		Mm.	°F.	(-0000)
1923	6.1	136	55.90	1,035
1924	4.1	133	50.70	484
1925	1.4	130	50.95	529
1926	2.5	130	52.50	833
1927	2.9	127	50.80	811
1928	3.4	130	51.25	1,227
1929	3.0	132	50.80	888
1930	3.1	138	52.30	601
1931	6.3	139	51.30	1,249
1932	6.0	142	52.15	1,323
1933	14.0	133	58.20	1,301
1934	2.0	120	49.90	468
1935	1.5	120	49.00	552
1936	3.8	129	51.20	794
1937	5.0	132	51.75	729
Mean	4.34	131.4	51.91	854.9
Mean without 1933	3.65	131.3	51.46	823.1

excluding the data for the 1933 brood. The resulting correlations are:

Ratio 3/4 smolts of same brood (Y)	3-year length (X_1)	June—July temperature (X_2)	Number 3 and 4 smolts migrating (X_3)
Correlations of Y with X's	0.7659**	0.6007*	0.6926**
Standard regression of Y on X's	.4456	.1836	.3461

$R=0.8314^{**}$.

The result is not altogether surprising. It shows that, except perhaps in years of extremely warm early summer temperatures, the temperature plays but a minor role.

Since temperature normally does not appear too important as a factor to induce migration, this variable was eliminated with the following result:

Ratio 3/4 smolts of same brood (Y)	3-year length (X_1)	Number of 3 and 4 year smolts migrating (X_2)
Correlations of Y with X's	0.7659**	0.6926**
Standard regressions of Y on X's	.5472	.3625

$R=0.8186^{**}$.

It will be noted that R is practically the same, .8186, as before, .8314, showing that temperature contributed little to the correlation.

Since number times individual weight equals the biomass of the smolts migrating it was of interest to examine the effect of biomass on the ratio migrating in the third year. The results are:

Ratio 3/4 smolts of same brood (Y)	3-year length (X_1)	Biomass migrating (X_2)
Correlations of Y with X's	0.7659**	0.7679**
Standard regressions of Y on X's	.4324	.4406

$R=0.8182^{**}$.

Length and biomass have a correlation coefficient of .7566. This close dependence of biomass on individual size suggests that the survival of the young may be linked with size.

However, at Bare Lake (Fish and Wildlife Service, 1955) the highest ratio 2.0 of 2 to 3 year smolts migrating from one brood (1948 to 1951 broods) was for the 1948 brood, when the total of all smolts migrating in the second year following spawning was 10,199, and the lowest ratio 0.2 was for 1949 when only 4,503 smolts left the lake in the second year after spawning. This occurred despite a progressive increase in smolt size.

APPENDIX K

PHOSPHORUS RELATIONSHIPS IN KARLUK LAKE

The 1927 determinations of soluble phosphorus in streams tributary to Karluk Lake (table A–15) as well as the determinations of total phosphorus both in Karluk Lake and in tributary streams are from Juday, Rich, Kemmerer, and Mann (1932). The 1935 and 1936 determinations of soluble phosphorus in streams (table A–15) are from Barnaby (1944).

If we make the wholly reasonable assumption that the 0.0105 milligrams/liter of soluble phosphorus during the week ending July 5 does not include any phosphorus from salmon carcasses, then it appears that the streams pick up a not inconsiderable quantity of soluble phosphorus between their upper reaches (last column, table A–15) and the lake. If we now subtract this average amount of 0.0105 from the averages of the subsequent weeks we can obtain a summation of the surplus during the summer of soluble phosphorus contributed by salmon carcasses decomposing in the streams.

This summation is 0.1721. The summation of the remaining 0.0105 by 52 weeks yields 0.5460, assuming that the soils are being leached at comparable rates during the remainder of the year. Since Nelson and Edmondson (1955) state that 25 percent of the salmon spawn in the lake and that one-third of the stream carcasses are either washed into the lake or removed by animals or birds, the figure for salmon-derived phosphorus must be doubled to represent the contribution of the carcasses. This gives 0.3442 as the relative contribution of carcasses against 0.5460 as the relative terrigenous contribution of soluble phosphorus. Since the spawning escapements of 1927, 1935, and 1936 averaged 1,041,000 salmon we can accept the 6,100 kilograms of phosphorus given by Nelson and Edmondson (1955) for one million spawners, which would leave an estimated 9,670 kg. (6,100 times 0.5460/0.3442) of soluble phosphorus contributed by the soils and rocks of the watershed.

Perhaps a more reliable method would be to consider only total phosphorus. The average

TABLE A–15.—*Soluble phosphorus in spawning streams tributary to Karluk Lake, 1927 and 1935–36*

[In milligrams per liter of water]

Streams	Taken near mouth during weeks ending on dates shown												Taken above spawning areas
	June	July				August					September		
	28	5	12	19	26	2	9	16	23	30	6	13	
d Creek													0.012 .015
ging Creek		0.002 .006		0.005			0.005	0.022		0.006		0.014	
raine Creek		.018 .032		.060 .130	0.060		.135	.022		.014		.030	.004
ttonwood Creek		.016 .015		.080 .045		0.030	.180	.020				.008 .014	
assy Point Creek			0.036 .056			.045		.016 .100				.014 .019	
ler Creek			.002 .016	.020		.025	.050	.016				.010 .012	
tle Lagoon Creek	0.004		.009 .010 .008	.016				.010					.005 .004 .006 .004
lfway Creek			.004 .010	.023		.025		.014 .040				.010	.002 .004 .004
mon Creek		.004	.016 .018	.060	.015		.005	.025 .050		.018	0.010		
per Thumb River		.007	.022 .020	.045	.025 .025		.019	.035 .070		.024	.026		.004
adow Creek		.012		.025		.030		.018 .060				.008	
scade Creek		.006 .003		.005 .024 .006		.016		.020 .025				.003	Trace.
nyon Creek		.032 .004		.008 .016				.030				.014	.002
lls Creek		.000 .000		.005 .006								.006	.003
m	.004	.157	.227	.556	.148	.171	.394	.593		.062	.036	.162	.069
ms	1	15	13	17	5	6	6	18		4	2	13	14
erage		.0105	.0175	.0327	.0296	.0285	.0657	.0329	(0.0242)	.0155	.0180	.0125	.0049
ove 0.0105			.0070	.0222	.0191	.0180	.0552	.0224	.0137	.0050	.0075	.0020	

otal phosphorus in the lake varied in 8 observations by Juday et al. (1932) from 0.014 to 0.019 gm./l. with very slight variation from the surface to the deepest part of the lake. Since the ake volume is 1,920 million cubic meters the total can be estimated at 31,680 kg.

Six observations of total phosphorus in streams ll above salmon spawning areas) yield an average of 0.0175 mgm./l. To estimate the amount ontributed by the streams an estimate must be nade of the total stream flow. Nelson and Edmondson (1955) estimate the mean outflow of Bare Lake (about 15 airmiles from Karluk Lake) t 6 cubic feet per second. The ratio of the Karluk watershed to that of the Bare Lake vatershed is about 93.68 (108.67 sq. miles/1.16 q. miles by planimeter measurement). From his we can estimate the average outflow of Karluk Lake at 562 c. f. s. The one measured ow we have available is 475 c. f. s. with the lake evel at −1 inch. Since from 1927 to 1953 the evel has varied from −13 to +18 inches we will ccept the 562 c. f. s. as a rough approximation of he true flow.

If the flow is 562 c. f. s., the total yearly outflow would be 656 million cubic yards or 502 million cubic meters. Since inflow must equal outflow the total natural phosphorus from the streams can be estimated at 11,480 kg. As the total phosphorus observations used were taken above the salmon spawning areas, thus eliminating the terrigenous phosphorus that would occur in the lower reaches of the streams, this seems to be a minimum estimate.

From the preceding figures we can make an approximate balance sheet for total kilograms of phosphorus in Karluk Lake (omitting phosphorus in the young salmon and other fishes in the lake) as follows:

	Kilograms
Estimated in Karluk Lake water	31,680
Estimated annual inflow from tributaries	11,480
Estimated annual gain from 1,000,000 carcasses	6,100
Total of chief sources	49,260
Minus loss from outflow (502/1,920 or 26.1 percent)	12,857
Remainder assuming 1,000,000 spawners	36,403
Remainder assuming 500,000 spawners	34,149
Remainder assuming 2,000,000 spawners	40,911

APPENDIX L

SPAWNING OF SOCKEYE IN KARLUK RIVER BELOW KARLUK LAKE

The extent of spawning in the main river below Karluk Lake may not have received as much attention as it may deserve because (1) such spawning often occurred rather late in the season and so was only partially observed by summer field parties visiting the lake, (2) since spawning fish would often be intermingled with fish migrating into the lake it was somewhat difficult to distinguish spawners from upstream migrants, and (3) because of the extremely small percentage of mature fish found that had stream-type scale nuclei indicating they had entered the sea as fry, it has been rather generally considered that the great majority of the offspring of these below-the-lake spawners perish.

Considerable doubt concerning this last point would seem warranted by the observations of Philip R. Nelson (loc. cit.) in which he saw fry ascending into the lake. Furthermore, the consistent negative effect of the number of pink-salmon spawners on the success of returns from sockeye spawners is difficult to wholly explain by competition for spawning beds within the lake and its tributaries, since few pinks entered the lake in years of small or moderate pink runs. If on the other hand, a significant number of sockeye normally spawn below the lake, and if the resulting young contribute a significant proportion of the seaward smolt migration, then the consistent negative effect of pink salmon spawners on the success of sockeye spawning has a more logical explanation as the pinks normally utilize the spawning beds below the lake.

Gilbert and Rich (1927, p. 30) write:

> . . . there are found in the river in spring and early summer a limited number of fry in their first year, which are believed to straggle out to sea during the early part of the season. Apparently they are not moving downward with the regular seaward migration of lake fish, but are observed even after the fingerling migration is past, in the eddies along the banks of the river and among the water weeds along the shore where the current is slack; but they seem to have disappeared before midsummer, and have doubtless gone to sea. . . . as considerable numbers of adult salmon are known to spawn in the river gravels below the lake it is considered probable that the fry in question have had this origin and that they occur numerously . . . . If this is true, their mortality in the sea must be extraordinarily great, for there are relatively few mature fish returning to spawn that have had this early history. In the 1926 run of mature fish, only six-tenths of 1 percent belonged to this group . . . .

Writing on the observations of Cloudsley Rutter, Chamberlain (1907) says of the Karluk:

> The upper course is of moderate current and affords excellent spawning ground, while in addition there are many sloughs to act as nursery ponds for the young.
>
> Throughout May and June [1903] the sloughs of the upper part of the Karluk River contained many sockeye fry or small fingerlings. In a haul May 22 nearly a thousand were taken, many with remnants of yolk. June 21 large schools of small fingerlings were numerous in the upper river, and some were taken with the dip net. June 30 a few fingerlings averaging nearly 2 inches in length were taken in a pool of the river.

Rutter attempted to determine whether any sockeye fry moved out of Karluk Lake down the river. Between June 5 and 28 he made 4 overnight sets with a net with a 25-foot spread in Karluk River at the lake outlet on the shoal side. Although the catch in the 4 sets included large numbers of sculpins and sticklebacks, 185 sockeye parr, and 39 trout, the nets also took on successive nights a few fry (16 fry, 2 fry, and no fry).

After Rutter's 1903 observations the next are those of Edward M. Ball in 1917 (Gilbert and Rich, 1927, p. 12):

> September 12 [1917].—This part of the river (the upper 2 miles) formed the spawning ground of a large number of red salmon, the river bottom being a mass of spawning beds.

O'Malley and Gilbert (Gilbert and Rich, 1927, p. 16) estimated a school of 10,000 sockeye at the foot of the lake in 1919, which they state was not present in 1921 (on Aug. 12).

In 1922, Gilbert and Rich (1927, p. 17) record sockeye spawning in greater abundance than pinks in the quarter-mile of river below the lake.

In 1924, Fred R. Lucas (Gilbert and Rich, 1927, p. 20) in the period September 16 to 24, wrote that sockeye in considerable numbers had spawned and were spawning in the river for one-half to three-quarters of a mile below the lake.

In 1926 (no spawning surveys were made in 1923 or 1925) Gilbert and Rich (1927, p. 26) wrote on August 27:

> . . . it was difficult to estimate the number of fish actually spawning in the upper 2 miles of the river, but I believe there were between 50,000 and 100,000. In addition, there were as many more, approximately, in the river passing up, either to spawn in the upper reaches of the river or to go on into the lake.

All of the information we have available is summarized in table A–16 which starts with 1917 and ns through 1932, the last year for which I had ld spawning observation notes. Out of 12 years ere are only 3 in which the notes fail to chronicle e spawning in the main river below the lake. In least 2 years (1926 and 1927) the spawners apar to have approached a quarter of a million.

There is some suspicion that most of these river awning estimates may be too low in some years cause of the sockeye that still remained to cend after the removal of the weir. In the 14 ars from 1922–36, inclusive (except 1924 when e number of pink salmon carcasses broke it rly), the weir was removed each year by the llowing dates: 1922 (October 22); 1926, 1927, 29 (October 14); 1923 (October 12); 1928 (October); 1930, 1933 (October 9); 1931 (October 8); 25 (October 6); 1932, 1934, 1935, 1936 (October .

For 4 of these 14 years the reports state that ature sockeye that had not yet ascended the river were still present in the brackish lagoon inside the river mouth when the weir was removed.

Furthermore, there is little information concern ing the spawning areas of a large portion of the late spawners during these years because the spawning ground observations were terminated long before all the spawners had had time to reach the lake as shown in the following tabulation:

Year	Date of last recorded spawning ground observations	Date of weir removal	Intervening days plus 11-day lag (lower weir to lake migration time)
1922	Aug. 22	Oct. 22	72
1923	[2]	Oct. 12	
1924	Sept. 24	Aug. 21[1]	?
1925	[2]	Oct. 6	
1926	Aug. 27	Oct. 14	59
1927	Sept. 22	Oct. 14	34
1928	Sept. 5	Oct. 11	47
1929	Sept. 12	Oct. 14	43
1930	Sept. 10	Oct. 9	40
1931	Sept. 27	Oct. 8	22
1932	Sept. 5	Oct. 5	41
Sum			358
Average number of days at end of season during which spawners counted through the weir could reach lake unobserved			44.8

[1] Weir washed out as a result of large number of pink salmon carcasses.
[2] No survey.

TABLE A–16.—*Sockeye spawning in Karluk River below Karluk Lake in certain years from 1917 to 1932*

ear of awning	Observer	Source of data	Area of spawning	Estimated number
1917	Edward M. Ball	Gilbert and Rich (1927)	Upper 2 miles	Large.
1918	No survey			
1919	O'Malley and Gilbert	Gilbert and Rich (1927)	At foot of lake	10,000.
1920	No survey			
1921	O'Malley and Gilbert	Gilbert and Rich (1927)	None up to Aug. 12	
1922	Gilbert and Rich	do	Upper ¼ mile	Greater abundance than pinks.
1923	No survey			
1924	Fred R. Lucas	Gilbert and Rich (1927)	Upper ½ to ¾ mile	Considerable numbers.
1925	No survey			
1926	Gilbert and Rich	Gilbert and Rich (1927)	Upper 2 miles	50–100 thousand and more coming on Aug. 27.
1926	Howard H. Hungerford	Warden report	1. Between lower weir and weir near Larsen Bay.	Many.
			2. Above Larsen Bay weir	150,000.
			3. Lower weir to lake total	250,000.
1927	Seymour P. Smith	Field notebooks	Upper 1½ miles	10–15 per 10 sq. yards, plus many already dead (158–238 thousand).
1928	S. P. Smith and Alan C. Taft	do	None mentioned	
1929	Merrill Brown (Boucher and Sundberg).	do	do	
1930	J. T. Barnaby	do	Lake down to Deep Hole	50–100 thousand on Sept. 10.
1931	do	do	Below lake	15,000 on Sept. 19, but one-third dead so is an underestimate.
1932	do	do	For 2 to 3 miles below lake	Two-thirds of 5,000 spawners on Aug. 31.

[1] Considerable numbers not yet ascended when weir removed on Oct. 14.
[2] Weir removed Oct. 9 with a few sockeye still in lagoon and river very low.
[3] Weir removed Oct. 8 with a few sockeye still in lagoon.

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